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FAUNAL SUCCESSION AND DEPOSITIONAL ENVIRONMENTS
WITHIN THE LODGEPOLE LIMESTONE (EARLY MISSISSIPPIAN)
OF SAMARIA MOUNTAIN, IDAHO

by

Gary Keith Hines

A thesis submitted in partial fulfillment
of the requirements for the degree

of

MASTER OF SCIENCE

in

Geology

Approved:

UTAH STATE UNIVERSITY
Logan, Utah

1981

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Gary Keith Hines

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ABSTRACT

Faunal Succession and Depositional Environments
within the Lodgepole Limestone (Early Mississippian)
of Samaria Mountain, Idaho

by

Gary Keith Hines, Master of Science

Utah State University, 1981

Major Professor: Dr. Richard R. Alexander
Department: Geology

Community succession, the orderly changes a community experiences with time, is considered to be the result of either autogenic or allogenic factors working singularly or in combination. It has been further suggested that, as communities undergo succession, certain biological parameters change in a predictable manner. Examination of members 2 through 4 of the Mississippian (Kinderhook-Osage) Lodgepole Formation of Samaria Mountain, Idaho provides a means to evaluate these concepts.

Within the study section comprised of 125 beds (61.5 m thick), four rock types are recognized. These include: (1) fossiliferous wackestone (78% of beds), which ranges in color from dark-gray (N3) to medium-light gray (N6), is fine to coarse crystalline, has an average insoluble content of 3.1 percent by weight, and an average organic content of 0.25 percent by weight; (2) fossiliferous mudstone

(15% of beds), which ranges in color from dark-gray (N3) to medium-gray (N5), is very fine to fine crystalline, has an average insoluble content of 2.3 percent and an average organic content of 0.30 percent by weight; (3) fossiliferous packstone (6% of beds), which ranges in color from medium-gray (N5) to light-gray (N7), is medium to coarse crystalline, has an average insoluble content of 3.3 percent by weight and an average organic content of 0.17 percent by weight; and (4) crystalline carbonate (1% of beds), which is light-gray (N7) in color, is coarse crystalline, has an insoluble content of 9.3 percent by weight, and an organic content of 0.2 percent by weight. However, at ninety-five percent confidence level, no statistical relationship could be seen between the rock types and either the insoluble contents or the organic content.

Twenty-one taxa, including corals, brachiopods, crinoids, blastoids, gastropods, echinoids, and sharks were recognized, with most taxa ranging throughout the study section. Well-preserved fossils are generally rare. However, this deficiency seems to be due to weathering of the containing strata rather than to currents acting on the skeletons prior to burial. Orientational data support this conclusion. Measurements of the direction (vector) from the apical end to the calical end of the horn coral Zaphrentis show that the orientations of toppled corals is random.

Two biological parameters are calculated for each of the bedding surfaces examined, i.e., diversity and calcified biovolume. Diversity is calculated two ways, i.e., in terms of equitability, and in terms of richness. For richness, values range from 0.0 to 7.41,

with a mean of 4.12, and for dominance diversity, values range from 0.0 to 1.95, with a mean value of 0.87. Calcified biovolume, which is used as the basis for inferences involving biomass, ranges from 0 to 30,015 cubic centimeters per bedding surface, with a mean value of 744.1 cubic centimeters per bedding surface.

Three faunal associations, as well as several sub-associations within the three major associations, are indicated by the clustering of indices of affinity. These associations include: (1) Zaphrentis-Crinoid-Syringopora-Echinoid-Cleiothryridina-Unispirifer-Spirifer-Orthotetes-Flexaria-Camarotoechia-Schizophoria-Lithostrotionella; (2) Cruziana-Dwelling tube; (3) Shark-Blastoid-Helminthopsis. Trophic relationships within the three associations suggest that they were the result of two factors: (1) the tendency towards a vertical stratification of the association's members, which resulted in a more efficient use of the water column; (2) direct physical interaction among association members, in the form of predator-prey or symbiotic relationships. The former type of interaction may have been operative between the sharks and blastoids of faunal association 3.

Environmental reconstruction involved the determination of four parameters: (1) paleocurrent direction and intensity; (2) sedimentation rate; (3) bathymetry; and (4) substrate. From the study of both physical and biological evidence, it is concluded that, during the time of Lodgepole deposition a very weak, unidirectional current, or multidirectional currents of similar competency operated over a carbonate-mud substrate. Evidence suggests that the sedimentation rate was extremely low, and that the $E_h = 0$ line was just below the

sediment-water interface. The water depth at this location was probably below normal effective wave base, but above the zone of oxygen depletion.

Study of fossils on bedding surfaces overlying barren bedding surfaces or surfaces containing fossil hash, suggests that four successional stages can be recognized. Because changes in the faunal composition between the various successional stages appear to take place both with (10 times), and without lithologic changes (16 times), it is concluded that succession may result from either biological modifications of the environment or physical changes. Therefore, succession was both autogenically or allogenicly controlled. Additionally, the communities were retrograded to an "earlier" successional stage 24 times within the 125 bed succession.

As succession proceeded through the successional sequence, values for equability-diversity and calcified biovolume generally increase. This trend is in agreement with previously predicted trends. With succession the overall trend observed in the trophic structure appears to be one of an increase in the proportion of filter feeders in the community relative to the proportion of deposit feeders in the community.

INTRODUCTION

Previous Work on Marine Paleocommunity Succession

The concept of a community has become the basic unit to synecological and paleontological studies. Over the years this concept has become a highly variable term, with the factors used to define a community varying from study to study. In defining a community, the following factors have commonly been used either singly or in some combination: the physical factors under which an organism can live, statistically recurrent groups in which an organism may be found, food resources which an organism may exploit, an individual's behavior patterns, and the habitat of an organism.

Johnson (1972, p. 152) defined a community in a very general way as an "... assemblage of species at a particular place and time." In contrast to such a general definition of a community, Kauffman and Scott (1976, p. 18), stated that the definition of any ecological unit should include statements concerning biotic composition, species interaction, environmental parameters, and unit boundaries. Taking these four elements into consideration they rigorously defined a community as

... a unique congregation of diverse organisms having a unique structure based on organism interaction and in some cases interdependence, as well as on energy flow; the community is adapted to and restricted by a particular suite of environmental parameters (physical, chemical, and biological). Communities can be of any size and are recurrent in space and time. They are bounded by sharp to gradually developed interfaces with other communities, from which they are in part biologically distinct. Community boundaries may represent

increased physiochemical and/or biological gradients, or in some cases may be formed by competition with other communities.

Kauffman and Scott realized, however, that logistics, preservation, and time constraints often restrict the use of such a detailed definition. Boucot (1975, p. 21), defined communities as recurring associations of taxa, with the recurring taxa being either independent of the presence or absence of other taxa within the recurring association, or dependent or interdependent on other taxa of the association in order to make possible the presence of more than one taxon.

The concept of recurring taxa will be used in this report to define a community. Boucot (1975, p. 29) stressed that what is defined by this method is "statistical entities, not necessarily functioning biologic entities." However, in support of this method, Kauffman and Scott (1976, p. 5) stated that

Complex evolution of biological characteristics, organism interrelations and thus structure of an ecological unit takes some time to develop, and occurs in response to a recurrent and/or long-term set of environmental parameters. It is possible, but unlikely, that any true ecological unit (especially communities and larger units) would have evolved only once, in one place, at one time.

Community evolution, the orderly changes which communities experience with time, is considered by many authors to be the result of one or the combination of two causes. First, communities evolve as a result of changes introduced by the organisms living within the community, and secondly, communities evolve as a result of physically induced changes in environmental parameters. Odum (1971) termed

these two causes of succession autogenic and allogenic succession, respectively.

In his paper on Niagaran reefs of the Great Lakes region, Lowenstam (1957), recognized three stages in the development of these reefs. These stages are: (1) the quiet-water stage, (2) the semi-quiet water stage, and (3) the rough-water or wave resistant stage. In going from the quiet water stage to the rough water or wave resistant stage, Lowenstam noted that there occurs an increase in the number of different species and in the population density. According to Nicol (1962), Lowenstam's three stages correspond to what is observed to take place in modern marine communities, and which in the terminology of modern ecology would be referred to as the pioneering, preclimax, and climax communities, respectively. In discussing evolution within Ordovician patch-reef communities, Alberstadt, Walker, and Zurawski (1974), recognized four stages. These stages are defined as follows: (1) a stabilization stage, in which a firm, clean-sand substratum was produced, possibly accompanied by a stabilization community; (2) a colonization stage, in which this accumulation is initially colonized by framework builders and encrusters that will participate in reef growth; (3) a diversification stage, during which the reef is populated by the greatest number of taxa; and finally (4) a domination stage, during which the build-up process continues, but is dominated by a single taxon.

Based on studies dealing with marine benthic communities, Johnson (1972) took the view that the evolution of these communities is largely controlled by the physical environment, and that physical

perturbations, in the form of deposition and erosion, that affect the species composition will result in the downgrading of a community to a previous stage of succession.

Odum (1971) observed that as evolution proceeds in terrestrial communities, several biological parameters change in a predictable manner (Fig. 1). In studying fossil communities in several stratigraphic sections, which range in age from Ordovician to Cretaceous, Walker and Alberstadt (1975) defined three types of succession, and tested some of Odum's observations concerning trends in biological parameters through successive stratigraphic stages (Fig. 2). From their study they concluded that Odum's observed trends appeared to apply to reefoid succession, short-termed succession, and long-termed succession in an unchanging physical marine environment. However, when dealing with long-term succession in a changing environment, Odum's observed trends concerning diversity did not appear to apply.

Objective and Procedure

The objective of this thesis will be to reconstruct the depositional environments of and faunal succession within a well-exposed section of the Early Mississippian Lodgepole Formation of Samaria Mountain, Idaho.

In the field, 125 consecutive bedding planes within a section 61.5 meters thick, were described. Field descriptions included information concerning crystallinity, color, and bed thickness, primary abiotic and biotic sedimentary structures present, the fossil taxa present and their abundances, the amount of

Ecosystem characteristic	Trend in ecological development early stage to climax or youth to maturity or growth stage to steady-state
Community Structure	
Species composition	changes rapidly at first, then more gradually
Size of individuals	tends to increase
Number species of autotrophs	increases in primary and often early in secondary succession; may decline in older stages as size of individuals increases
Number species of heterotrophs	increases until relatively late in the sere
Species diversity	increases initially, then becomes stabilized or declines in older stages as size of individual increases
Total biomass	increases
Nonliving organic matter	increases
Energy Flow (Community Metabolism)	
Gross production (P)	increases during early phase of primary succession; little or no increase during secondary succession
Net community production (yield)	decreases
Community respiration (R)	increases
P/R ratio	$P > R$ to $P = R$
P/B ratio	decreases
B/P and B/R ratios (biomass supported/unit energy)	increases
Food-chains	from linear chains to more complex food webs
Biogeochemical Cycles	
Mineral cycles	become more closed
Turnover time	increases
Role of detritus	increases
Nutrient conservation	increases
Natural Selection and Regulation	
Growth form	from r -selection (rapid growth) to K -selection (feedback control) ^a
Quality of biotic components	increases
Niches	increasing specialization
Life cycles	length and complexity increases
Symbiosis (living together)	increasingly mutualistic
Entropy	decreases
Information ^b	increases
Overall stability	increases

Figure 1. Predicted trends in biological properties for a community undergoing succession (Odum, 1971).

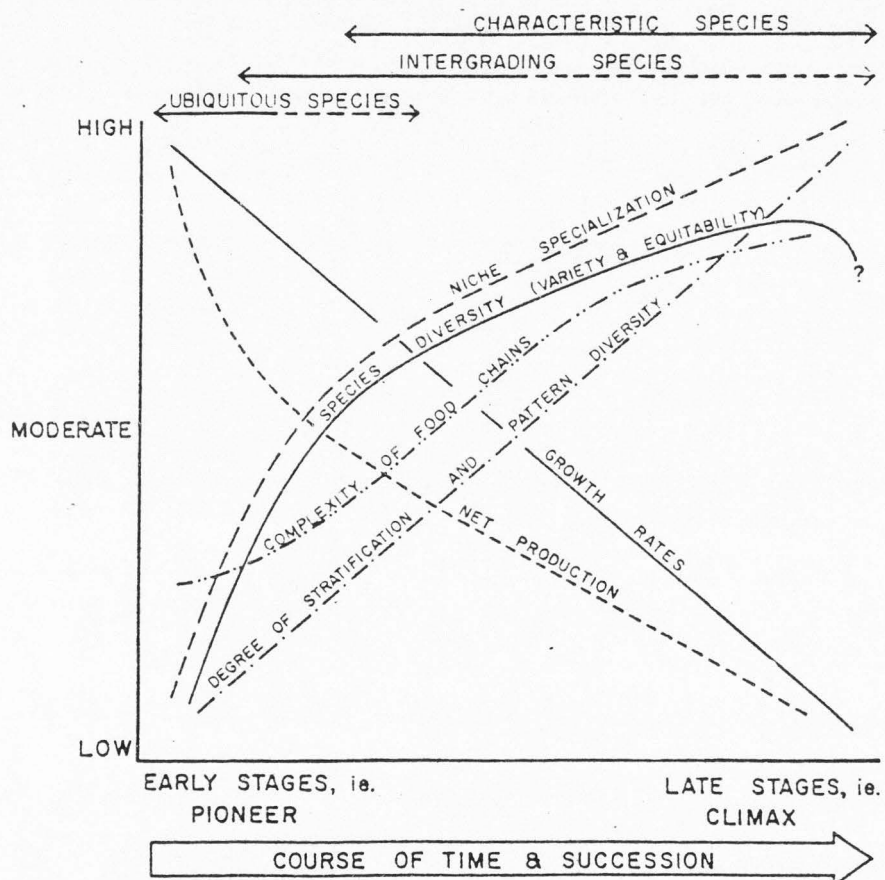


Figure 2. Some expected changes in community structure during ecological succession (Walker and Alberstadt, 1975).

disarticulation, fragmentation, and the orientation of the various fossil taxa, and the amount of surface area examined on each bedding surface. Lithologic samples were taken from each bedding plane examined along with representative samples of each fossil taxon.

Procedures followed in the laboratory included the acid-digestion of the lithologic samples to obtain the insoluble residues and preserved organic matter, x-ray diffraction of powdered samples, calculation of the species diversity (richness and equitability) for each bedding surface, calculation of the calcified biovolume for the fossil assemblage of each bed, graphic illustration of paleocurrent information, reconstruction of the trophic structure for the various stages of succession, and the determination of the faunal associations through the calculation of an index-of-affinity matrix and the use of cluster analysis.

The synthesis of these data will provide the basis for inferences concerning water depth, turbidity, sedimentation rate, current intensity, and the Eh and pH. It will also provide the means to evaluate the concepts of autogenic and allogenic succession, and trends in biological parameters within faunal succession (Odum, 1975, p. 156; Walker and Alberstadt, 1975, p. 239), stages in community evolution (Lowenstam, 1957, pp. 215-248; Nicol, 1962, pp. 172-176; Alberstadt, et al., 1974, pp. 1179-1180; and the retrogression of a community to an earlier stage of succession due to physical perturbation (Johnson, 1972, p. 153).

Location and Accessibility

The section of the Lodgepole Formation under consideration in this study is located along an east-west trending divide between Gardner and Henderson Canyons, approximately two kilometers north and five kilometers west of Woodruff, Idaho (S1/2, SW1/4, Sec. 12, T. 16 S., R. 35 E., Samaria Quadrangle, Idaho-Utah) (Fig. 3). Access to the study section is possible by means of an unimproved dirt road within Gardner Canyon. The Lodgepole at this location has been previously measured and described by Beus (1963; 1968). At this location, the Lodgepole Formation crops out as a series of ledges which dip gently (18°) to the west and alternate with covered intervals (Figs. 4, 5, and 6).

Stratigraphy and Biostratigraphy

According to Beus (1963), the name Lodgepole Limestone was first applied by Collier and Cathcart (1922, p. 173) to the lower unit of the Madison Group (Peale, 1893), from exposures in the Little Belt Mountains of Montana. The name Madison, which has been retained as a group named in Montana, has been used as a formation name for the early Mississippian rocks in northern Utah, southeastern Idaho, and Wyoming. Because of lithologic and faunal similarities between the Lodgepole Limestone of Montana and Madison Formation of northern Utah and southeastern Idaho, many authors, including Williams (1943), Holland (1952), and Beus (1963), have recommended that the Madison Formation would be better referred to as the Lodgepole Limestone. In



Figure 4. The Lodgepole Limestone at the study section:
west view.

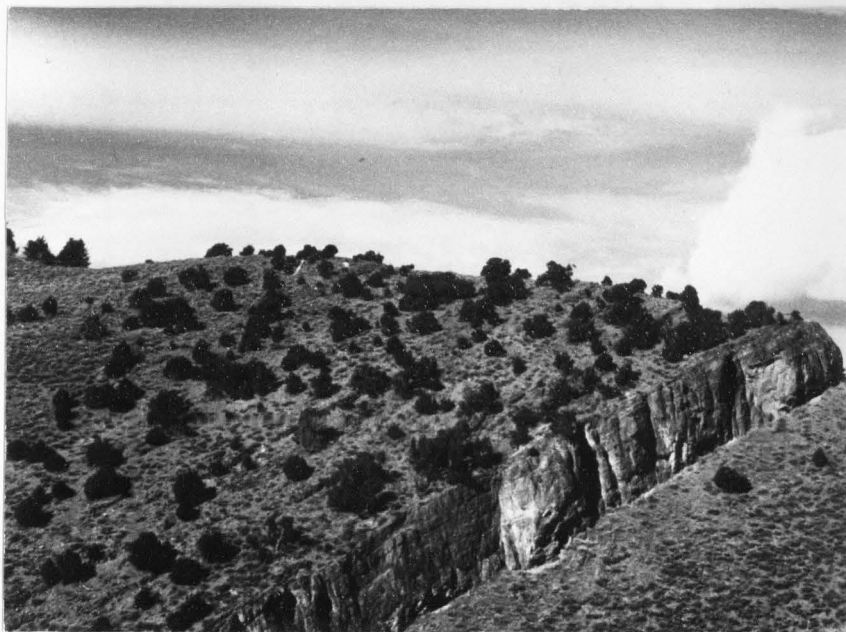


Figure 5. The Lodgepole Limestone at the study section:
north view.

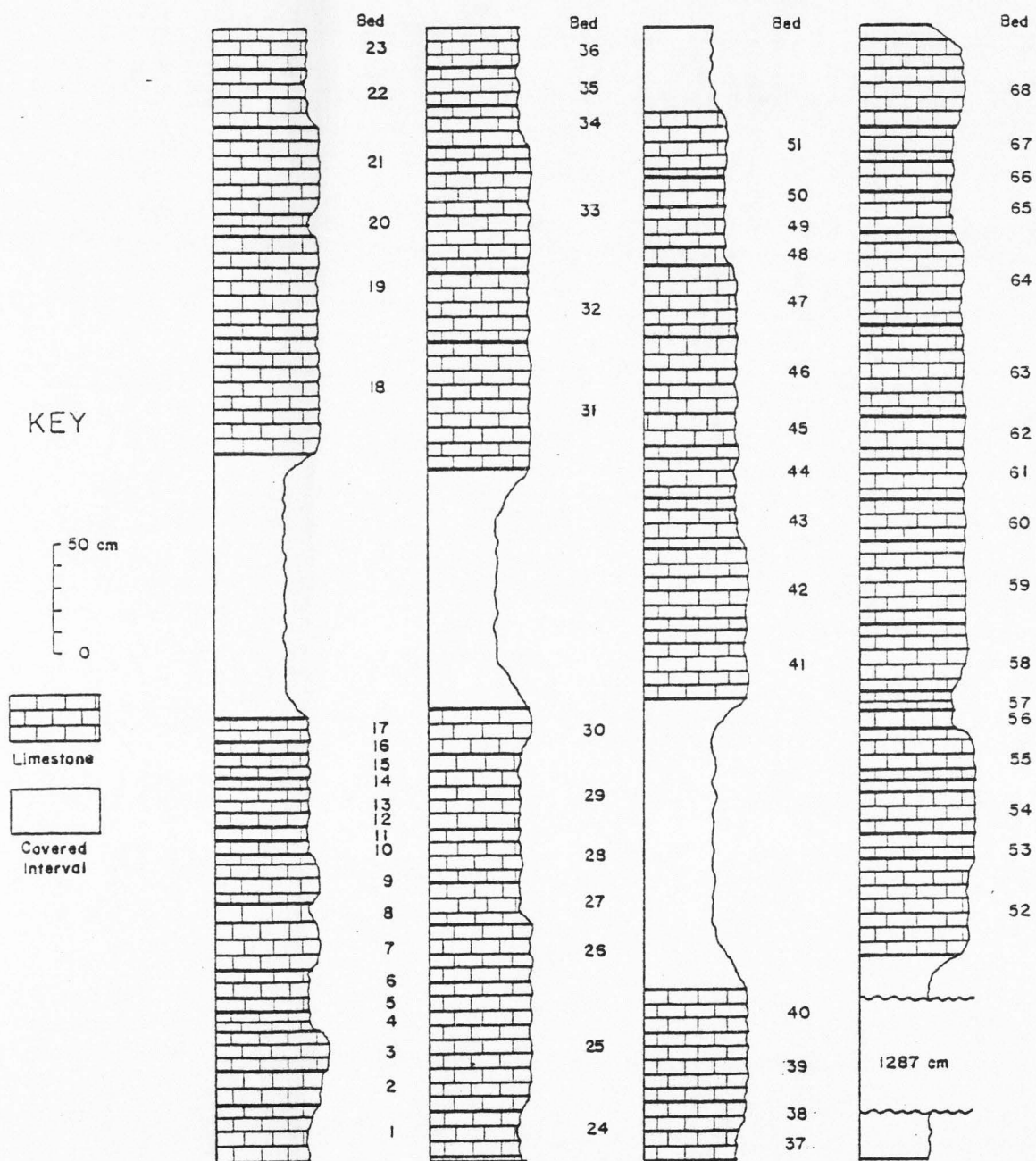


Figure 6. Stratigraphic section of the Lodgepole Formation of the study section.

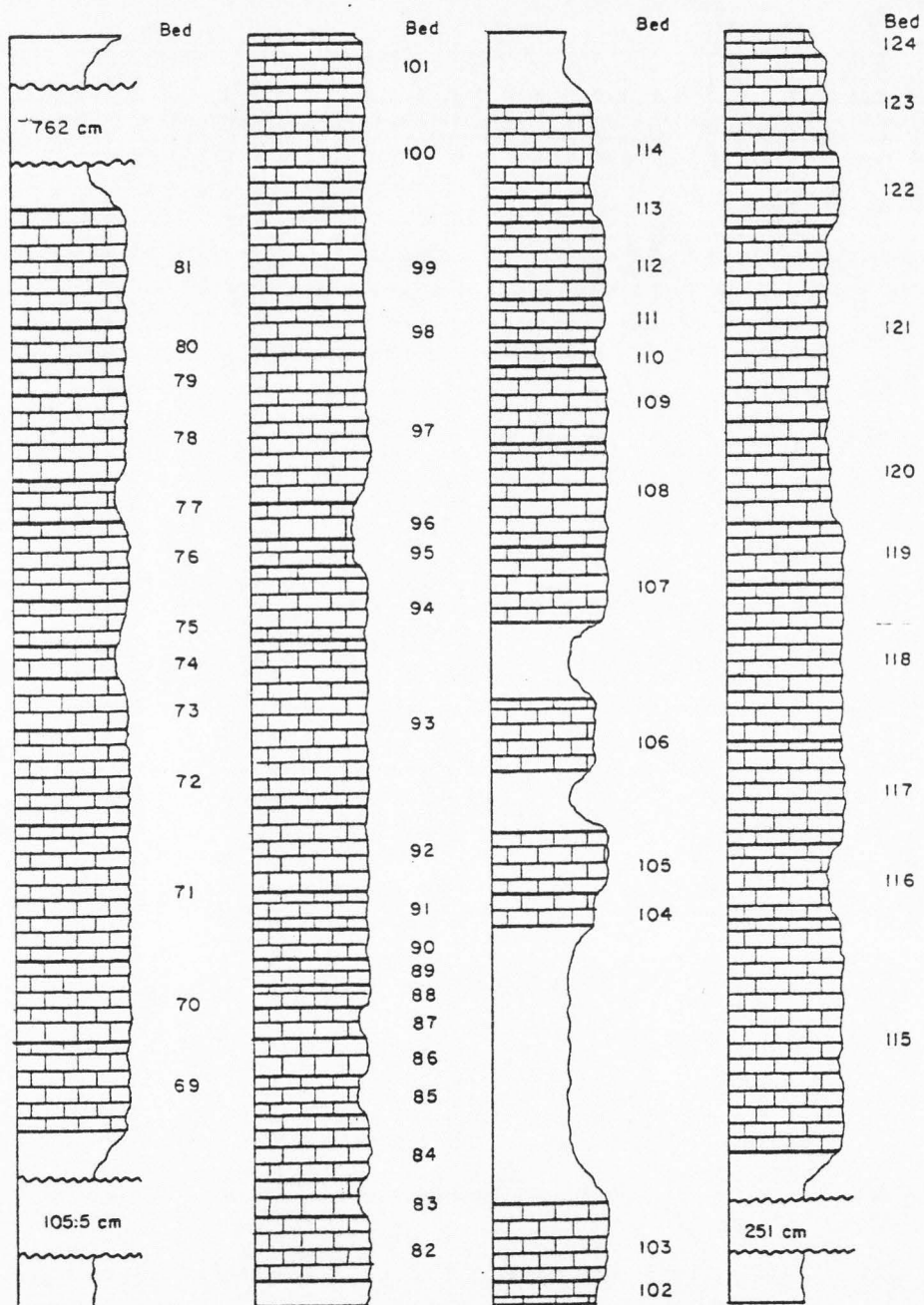


Figure 6. Continued.

a study of Carboniferous formations in southeastern Idaho and northeastern Utah, Williams (1943, p. 619) stated that

... the sections of the Madison Formation from one end of the study area to the other are so uniform in lithologic character and fauna that there is little doubt that the formation was deposited synchronously throughout the region.

The fauna, according to Williams, is indicative of an early Mississippian age for the Madison. Holland (1952), in working with the Madison Limestone at Leatham Hollow, northern Utah, found fossils which he interpreted to be of Kinderhookian age, but indicated that Osagean fossils typical of the Mississippi Valley are absent. Beus (1968, p. 791) stated that "Unispirifer centronatus is the most abundant brachiopod element in units 2 and 3 of the Lodgepole of southeastern Idaho and northern Utah, and is indicative of Kinderhook or Osage age." He also indicated that the presence of Spirifer rowleyi in unit 4 suggests an age equivalent to the Fern Glen (earliest Osagean) for this unit (1968, p. 792). In a study of the microfauna of the Lodgepole of southeastern Idaho, Wyoming, and Montana, Sando, Mamet and Dutro (1969) found that two foraminiferal assemblages can be recognized. These two assemblages were found to correspond to Zone pre-7 and Zone 7 of the Global Foraminifera zones and therefore indicate an age of early Kinderhook to latest Kinderhook for the Lodgepole. Rose (1976) stated that his lower depositional complex, of which the Lodgepole Limestone is the lower transgressive phase, ranged in age from early Kinderhookian to early Meramecian. Within the top 26.5 feet of the Lodgepole Limestone at their Little Flat Canyon section (southeastern Idaho), Sando, Dutro,

Sandberg, and Mamet (1976), found corals, brachiopods and conodonts which indicated an age of early Osagean. Skipp, Sando, and Hall (1979) indicated that foraminifera, conodonts and corals have been used to determine an age of Kinderhook to early Osage for the Lodgepole. Roberts (1979) indicated that the Madison Group of southeastern Montana is divided into two formations, the Lodgepole Limestone and the Mission Canyon Limestone, with a Kinderhook to early Osage age assigned to the Lodgepole and an age of late Osage to Meramec assigned to the Mission Canyon.

Paleogeography

During early Mississippian time, five major structural features dominated in the western United States (Fig. 7). The first of these features is the Transcontinental Arch, which was emergent at this time and extended from Canada to New Mexico. Bordering the Transcontinental Arch to the west was the Cordilleran platform, which was a broad cratonic area upon which relatively thin deposits of carbonates and evaporites were laid. To the west of this platform were positioned the Cordilleran Miogeosyncline, the Antler Orogenic Belt and the Cordilleran Eugeosyncline. According to Roberts (1979), the area of southeastern Idaho and north-central Utah was the site of a north-trending hingeline between the shelf and the miogeosyncline. With time, this hingeline migrated to the east, so that during Kinderhookian time the study area was part of the shelf, but by Chesterian time the area was part of the geosyncline. This shift of the hingeline to the east can be recognized in the rock record. Welsh

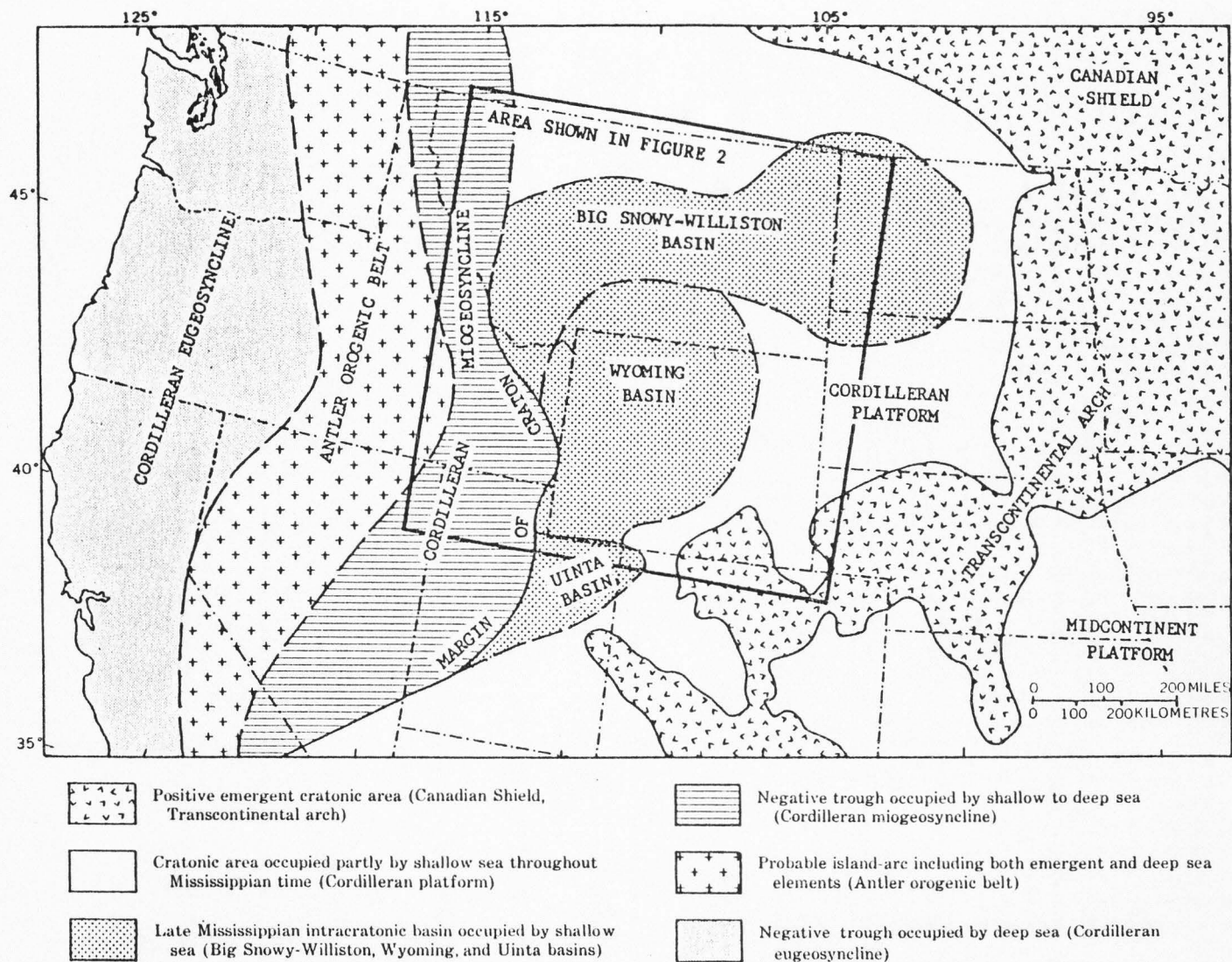


Figure 7. Major structural features of the western United States during the Mississippian (from Sando, 1976, p. 318).

and Bissell (1979, p. Y17) stated that "... all units [upper Lodgepole and its lithostratigraphic equivalents] are characterized by dark-gray, thin-bedded limestones and abundant bedded and nodular chert. These clinoform units were deposited in deeper water than the earlier Mississippian limestones.

According to most authors (Williams, 1948; Rose, 1976; Sando, 1976; Roberts, 1979; and Skipp, Sando and Hall, 1979), the Lodgepole Formation was deposited under transgressive conditions. For the Mississippian of the western United States, Sando (1976) recognized two periods of deposition (Cycles 1 and 3) which are separated by a period of erosion (Cycle 2). He further divided the cycles into phases which represent changes in depositional patterns. Deposition of the Lodgepole occurred during phases 1 through 4 of Cycle 1. Sando (1976, p. 321-323) described the depositional conditions which existed during these phases in the following way:

Cycle 1, phase 1--Early Kinderhookian: "As the Mississippian sea advanced rapidly onto the Cordilleran platform, over a terrane composed of Cambrian, Ordovician, and Devonian rocks, terrigenous and carbonate sediments were deposited in several marine basins separated by low-lying land."

Cycle 1, phase 2--Late Kinderhookian: "In phase 2, continued rapid transgression of the Cordilleran sea brought about the initiation of shelf carbonate deposition on the Cordilleran Platform."

Cycle 1, phase 3--Latest Kinderhookian: "Phase 3 marked the height of the Cycle 1 transgression and was characterized by marked differentiation of the sea into shelf, slope, and trough. The lithofacies belts are similar to those of the previous phase, but the shelf margin shifted landward, probably because of a rise in sea level."

Cycle 1, phase 4--Early Osagean: "During this period progradation of shelf carbonates caused the shelf margin

to migrate seaward over the slope, so that slope deposits cannot be distinguished. Most of the shelf was characterized by cyclical subtidal and intertidal carbonate sediments that record many minor transgressions and regressions of the sea."

LITHOLOGIC ANALYSIS

General Description

In describing the Lodgepole at the location of this study, Beus (1963; 1968) recognized four members which he informally designated, from bottom to top, as members 1, 2, 3, and 4. These members were differentiated on the basis of their topographic expression, with member 1 forming a prominent cliff known locally as the "Chinese Wall," member 2 being a slope former, member 3 forming a series of ledges, and member 4 forming a partially covered slope. The section under consideration in this study begins within Beus' member 2, and extends to the top of the 4th member.

Four major rock types were recognized in this study. The dominant rock type, comprising 78% of the beds examined, were composed of fossiliferous wackestone (Dunham, 1962), which ranges in color from dark-gray (N3) to medium light-gray (N6), is very fine crystalline to coarse crystalline, and is commonly structureless, laminated, or cross-stratified. The second most abundant rock type, comprising 15% of the beds examined, is fossil-bearing mudstone, which ranges in color from dark-gray (N3) to medium-gray (N5), is very fine crystalline to fine crystalline, and is either structureless or laminated. Third in abundance, composing 6% of the beds, is fossiliferous packstone, which ranges in color from medium gray (N5) to light gray (N7), is medium to coarse crystalline, and is either

laminated or structureless. The fourth rock type, which comprises 1% of the beds examined, is crystalline limestone, which is light gray (N7) in color, coarsely crystalline, and structureless. Dark gray (N3) chert nodules which are elongate parallel to bedding and generally situated along bedding surfaces, can be found associated with all four rock types found in the study area. For individual bed descriptions, see Plate 1.

Analysis of Insoluble Residues

The insoluble residue content was determined for samples taken from each of the 125 beds examined. The procedure followed was to break approximately thirty grams of each sample down into pebble size fragments. These fragments were then placed into a Bico Type UI Pulverizer which further reduced the sample to a fine powder. This size reduction was done in order to speed up the dissolution of the sample. Samples were then weighed to the nearest hundredth of a gram, and placed in a solution of 10% hydrochloric acid. Once effervescing ceased, and the remaining material was allowed to settle, the solution was decanted and replaced with a fresh solution of 10% hydrochloric acid. This procedure was repeated until no visible signs of a reaction could be seen. The remaining material was then rinsed twice with deionized distilled water and dried for twelve hours in an oven set at 60°C. The samples were then removed from the oven, allowed to come to room temperature and reweighed.

The insoluble-residue-analysis provides the basis for inferences concerning the paleo-environment in the following ways:

1. Low amounts (weight percent) of insoluble residue may indicate considerable distance from a source area, i.e., the shoreline.

2. Low amounts (weight percent) of insoluble residue may indicate agitated conditions, i.e., in the zone of intense winnowing by wave and current action.

3. Low amounts (weight percent) of insoluble material may indicate a low influx of terrigenous material.

The insoluble residue content of the 125 samples examined in this analysis ranged from 0.5 to 9.5% of the sample by weight, with the mean value being 3.1% (see Plate 1). The range and mean values of the insoluble residue content for each of the four rock types are as follows: mudstones--0.85 to 3.8%, 2.3%; wackestone--0.5 to 9.5%, 3.1%; packstone--0.9 to 6.3%, 3.3%; and crystalline carbonate--9.3%, 9.3%. However, a one-way analysis of variance, using an F-test, showed that, at a 95% confidence interval, the mean values for the insoluble content for the various rock types are statistically indistinguishable.

Organic Residue Analysis

A determination of the organic content was made on the same 125 samples used for the insoluble-residue analysis. Once the amount of insoluble residue was determined, a 5.25% solution of sodium hypochlorite (Clorox) was added to oxidize the organic material present. This solution was allowed to remain in contact with the insoluble residue for 48 hours before it was decanted. The remaining

material was rinsed four times with deionized distilled water and dried for twelve hours in an oven set at 60°C. After being removed from the oven, the sample was allowed to come to room temperature and then was reweighed. Data resulting from this analysis will provide the basis for inferences made concerning the Eh conditions at or beneath the substrate surface during or shortly after the time of deposition.

Results of this analysis (Plate 1) show that the organic content within the 125 samples ranged from 0.05 to 1.07% of the sample by weight, with a mean value of 0.26%. Ranges and means for the four rock types found in the study area are as follows: mudstones--0.07% to 0.49%, 0.30%; wackestones--0.05% to 1.07%, 0.25%; packstones--0.06% to 2.8%, 0.17%; and crystalline carbonate--0.2%, 0.2%. A one-way analysis of variance using an F-test showed that the mean values for the organic content of each of the four rock types are not statistically different.

X-ray Analysis

Following the determination of the amount (weight percent) of organic matter, the remaining insoluble residue was analyzed for hematite and pyrite through the use of X-ray diffraction. The insoluble residue was first made into a slurry by the addition of deionized distilled water. Two to three drops of this slurry were placed on a glass slide, and the water allowed to evaporate. Once the water evaporated, the slides were placed in a Siemens X-ray diffractometer and exposed to copper K α radiation. X-ray diffraction

patterns were produced from runs between 20° and 35° , in order that the major hematite peak at 24.2° and the major pyrite peak at 33.1° . Results from this analysis will provide the basis for inferences made concerning Eh conditions at or below the substrate surface, at or near the time of deposition.

Results of this analysis indicate the probable presence of hematite in beds 6 and 41, with beds 8, 67, and 85 showing its possible presence. The probable presence of pyrite was indicated in only one sample, that from bed 114.

FAUNAL ANALYSIS

Composition

Twenty-one different taxa were recognized in the field throughout the studied section. Of these, eight taxa belong to the phylum Brachiopoda, four belong to the phylum Coelenterata, three to the phylum Echinodermata, and one each to the phyla Mollusca and Chordata. The remaining four taxa are represented by traces formed as the result of the feeding or dwelling activities of various organisms. Taxa were identified as closely as possible: coelenterates, molluscs, and brachiopods were identified to the genus level, and echinoderms and chordates were identified to the class level, when possible. Brief descriptions of each taxa are as follows:

Lithostrontionella is a massive ceroid hemispherical shaped colonial rugose coral, composed of prismatic corallites which have diameters up to 3 centimeters. Lithostrotionella ranges from bed 44 to bed 113 (Fig. 8).

Zaphrentis is a ceratoid shaped solitary rugose coral with a single fossula within a deep calyx; septa are numerous and extend to the center of the calyx. Zaphrentis ranges from bed 6 through bed 113 (Fig. 9).

Syringopora is a fasciculate tabulate coral, with delicate corallites, which range from 1 to 3 millimeters in diameter.

Syringopora is generally found in the form of fragmented corallites,

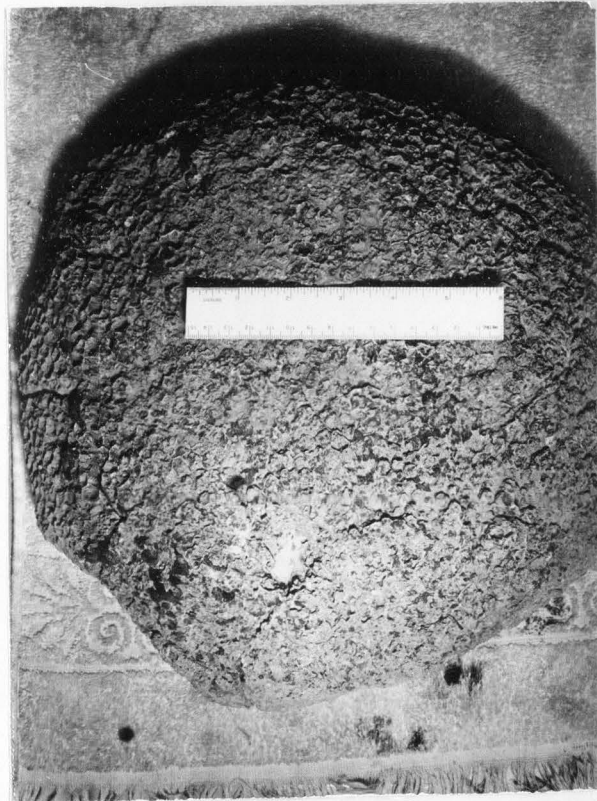


Figure 8. The colonial rugose coral Lithostrotionella.

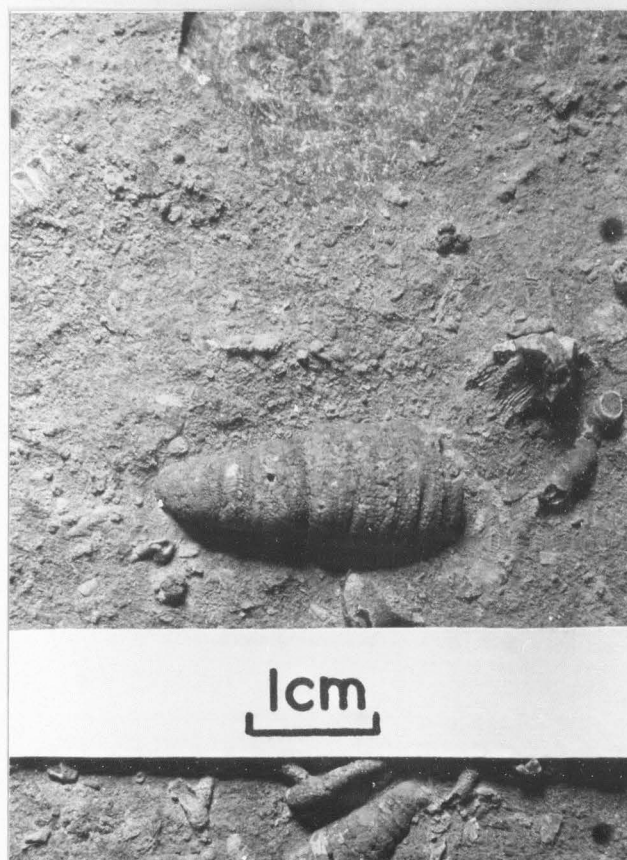


Figure 9. The horn coral Zaphrentis.

although it may occasionally be found in the form of a hemispherically shaped corallum. Syringopora ranges from bed 2 to bed 115 (Fig. 10).

Aulopora is a small, delicate tabular coral consisting of trumpet-shaped corallites with diameters up to 1 millimeter. Coralla consist of multiserial rows of corallites. Aulopora was found on two bedding surfaces, bed 6 and bed 7.

Euomphalus is a subdiscoidal gastropod with a slightly elevated spire. The whorls have a well-defined angulation on the upper-outer edge and a lower surface which is rounded to slightly angular. It is most commonly found as an outline on bedding surfaces. Unweathered complete specimens are rare. Euomphalus ranges from bed 7 to bed 113 (Fig. 11).

Unispirifer is a strongly transverse, biconvex, articulate brachiopod which has a hingeline that is equal to the maximum length of the shell. Narrow fold and sulcus are present, along with numerous simple costae. Unispirifer ranges from bed 7 to bed 124 (Fig. 12).

Spirifer is a large, biconvex, articulate brachiopod, in which the hingeline is shorter than the maximum width of the valves. Valves are transversely subelliptical in outline and are covered with flattened plications. Spirifer is most commonly found as outlines on the bedding surface, with whole specimens never being found. Spirifer ranges from bed 41 to bed 123.

Camarotoechia is a small, biconvex, articulate brachiopod, which is subtriangular in outline. The surfaces of both valves are costate, with a well-defined sulcus and a slightly less well-defined

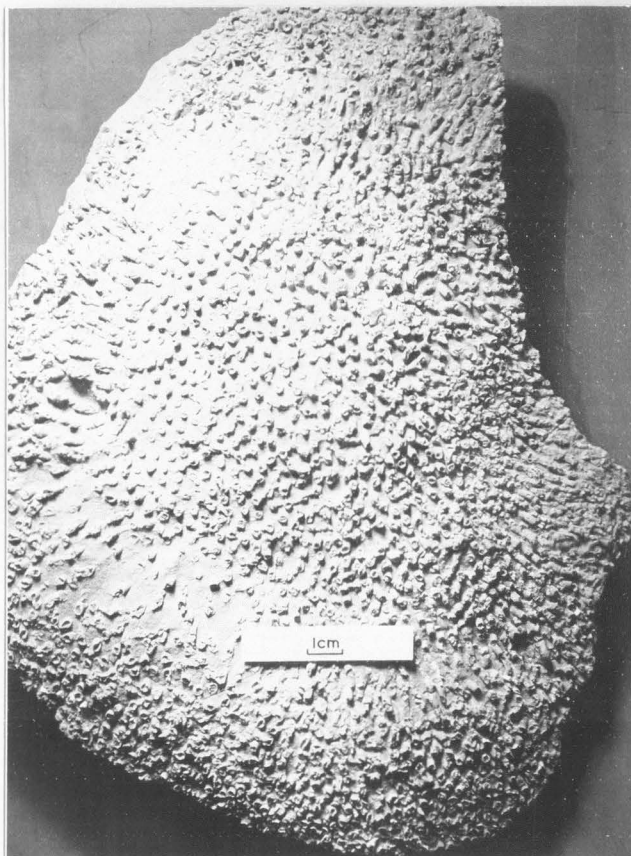


Figure 10. The tabulate coral Syringopora.



Figure 11. The gastropod Euomphalus.

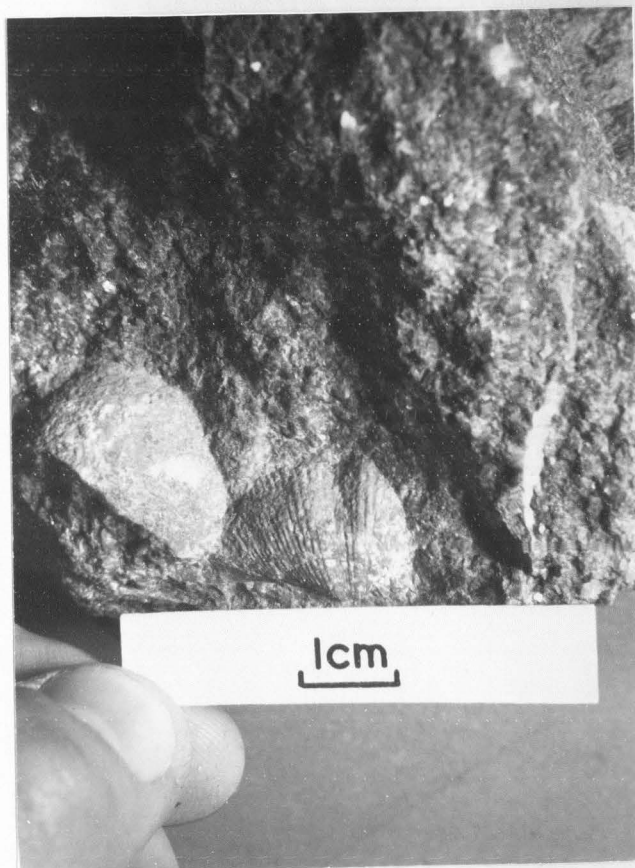


Figure 12. The brachiopod Unispirifer.

fold; valves are slightly inflated in the umbonal region, and the commissure is undulated. Camarotoechia ranges from bed 27 to bed 113 (Fig. 13).

Composita is a biconvex, articulate brachiopod which is subtriangular in outline. The shell surface is smooth, with a low fold and shallow sulcus. Composita was found on three bedding surfaces, bed 2, bed 63, and bed 116 (Fig. 14).

Cleiothyridina is a small, subequally biconvex brachiopod, with a subcircular outline. Valve surfaces are covered with lamellar extensions at the growth lines. Cleiothyridina ranges from bed 7 to bed 67 (Fig. 15).

Flexaria is a medium-sized concavo-convex, subquadrate, articulate brachiopod; the surface of which is covered with prominent discontinuous costae, and short spine ridges on flanks. Flexaria is found on six bedding surfaces, ranging from bed 44 to bed 118 (Fig. 16).

Schizophoria is a large, subrectangular to subelliptical, articulate brachiopod, with a low dorsal fold and ventral sulcus. Surface is finely costellate. Schizophoria is found on eight bedding surfaces, ranging from bed 84 to bed 114 (Fig. 17).

Orthotetes is a large biconvex to plano-convex, finely costellate, umbonally cemented articulate brachiopod. Orthotetes ranges from bed 6 to bed 101, (Fig. 18).

Crinoids are found as disarticulated columnals or in short, articulated stem segments, calices were not found. Columnals are circular in outline, with a circular lumen and a wide crenularium. Crinoids range from bed 2 to bed 125 (Fig. 19).



Figure 13. The brachiopod Camarotoechia.

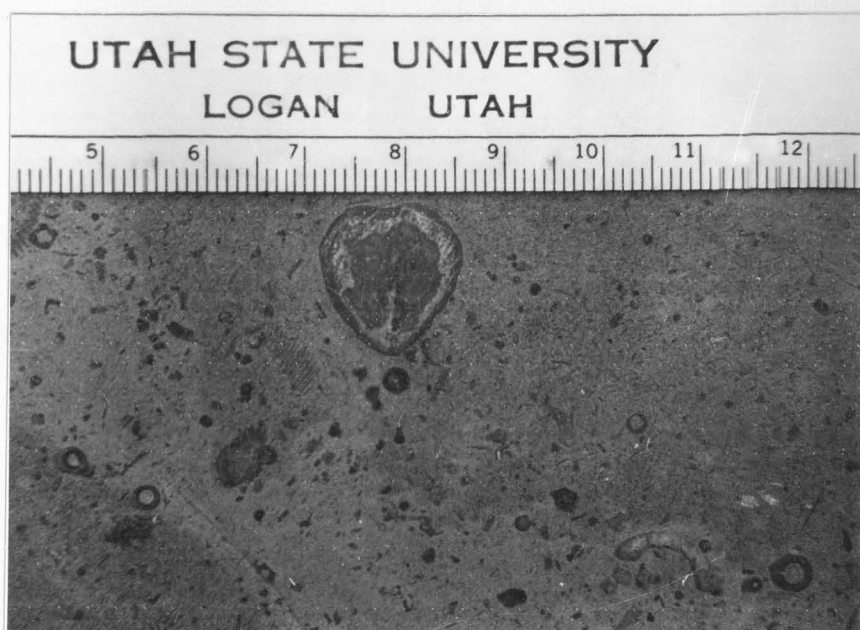


Figure 14. The brachiopod Composita.

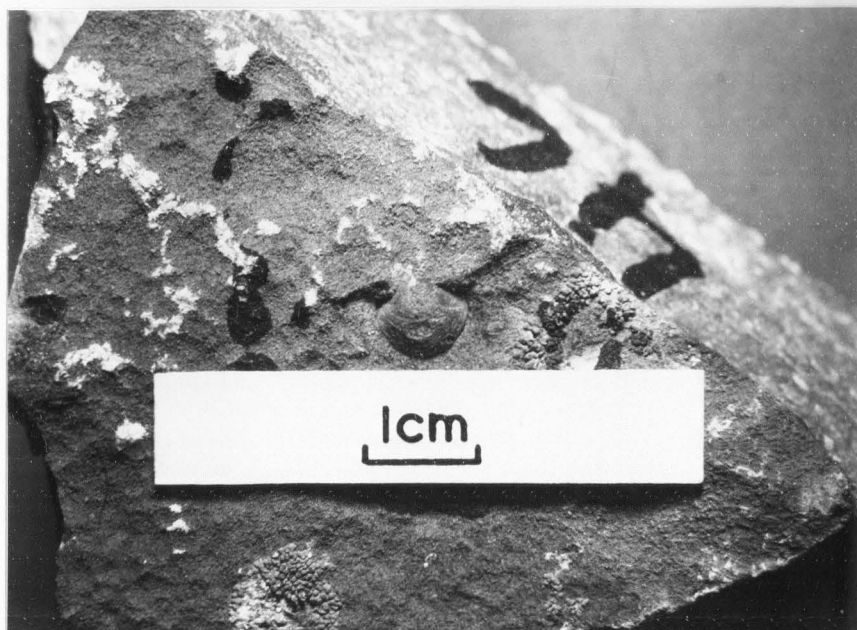


Figure 15. The brachiopod Cleiothyridina.

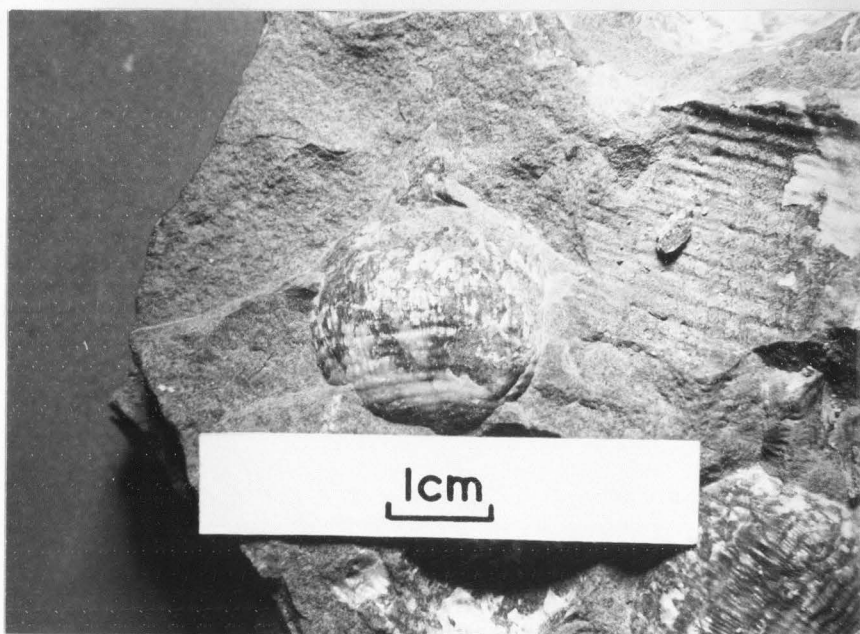


Figure 16. The brachiopod Flexaria.

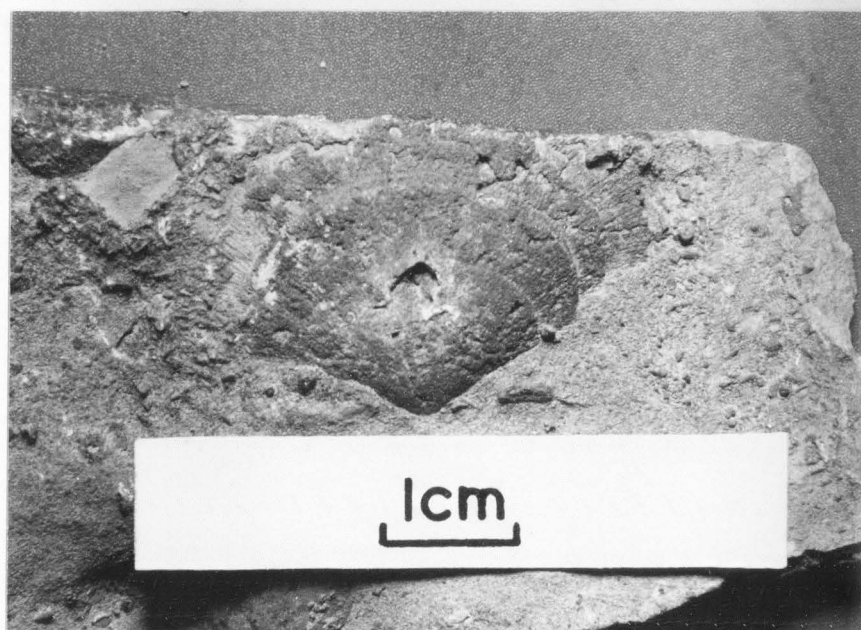


Figure 17. The brachiopod Schizophoria.

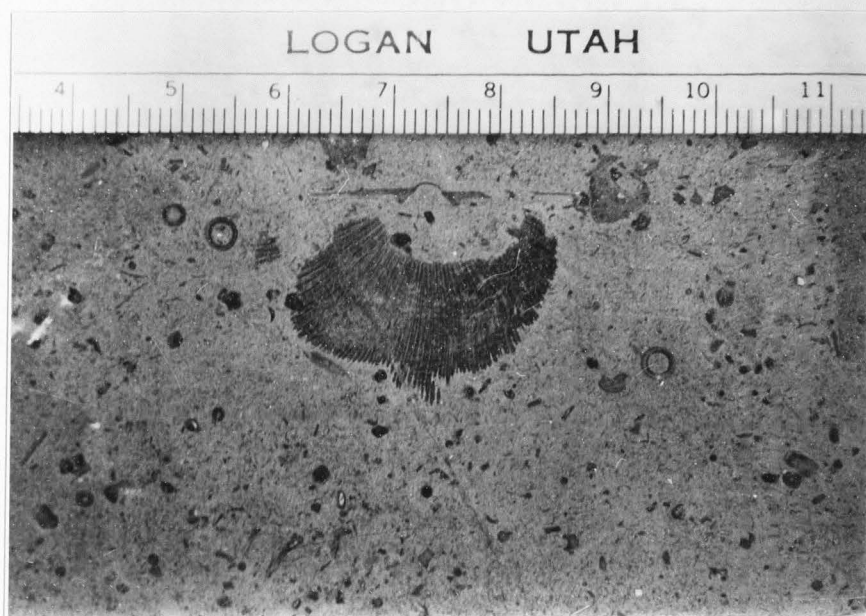


Figure 18. The brachiopod Orthotetes.

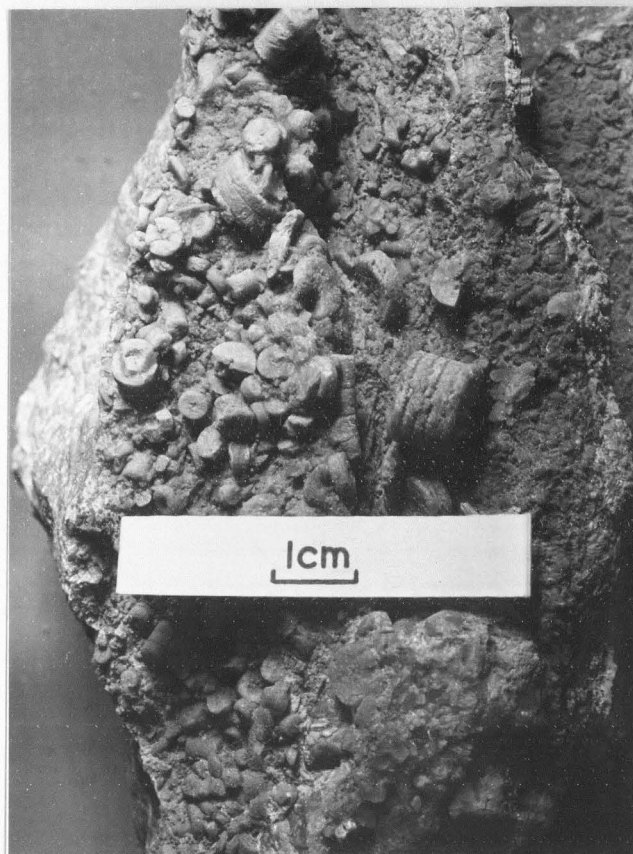


Figure 19. Crinoid columnals.

Blastoids are found as disarticulated columnals only. Columnals have a circular outline with a stelliform-shaped lumen. Blastoids are found only in bed 125 (Fig. 20).

Echinoid Spines are short spines filled with a loose, calcareous mesh (Fig. 21).

Cruziana is a trail-like trace on a bedding surface, with transverse ornament. Cruziana were found on three bedding surfaces, beds 41, 83, and 97 (Fig. 22).

Zoophycus is a spiraled structure consisting of concentric feeding traces on a bedding surface. Zoophycus was found only on bed 85 (Fig. 23).

Helminthopsis is a simple, trail-like meander on a bedding surface. This trace fossil was found on beds 42, 95 and 125 (Fig. 24).

Dwelling tubes are vertical burrows narrowing towards the base. Dwelling tubes were found only on bed 41.

Sharks are represented by teeth which are black, subtriangular in shape, and have a low enlarged crown which is specialized for grinding. The surface of each tooth has a pitted appearance, due to numerous parallel, vertical tubes of dentine, which form the crown of the tooth. Shark teeth are found on two bedding surfaces, namely bed 112 and bed 125 (Fig. 25).

Fragmentation and Disarticulation

Holland (1952), in his discussion of Mississippian rocks of the Rocky Mountains, noted that at Leatham Hollow, Utah, that the Lodgepole Limestone is fossiliferous throughout. However, he also

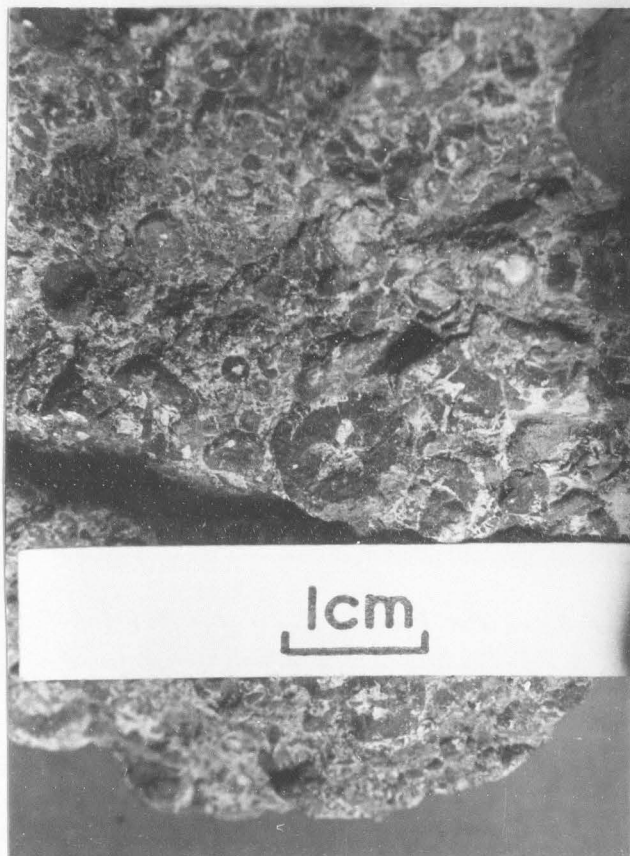


Figure 20. Blastoid columnal.

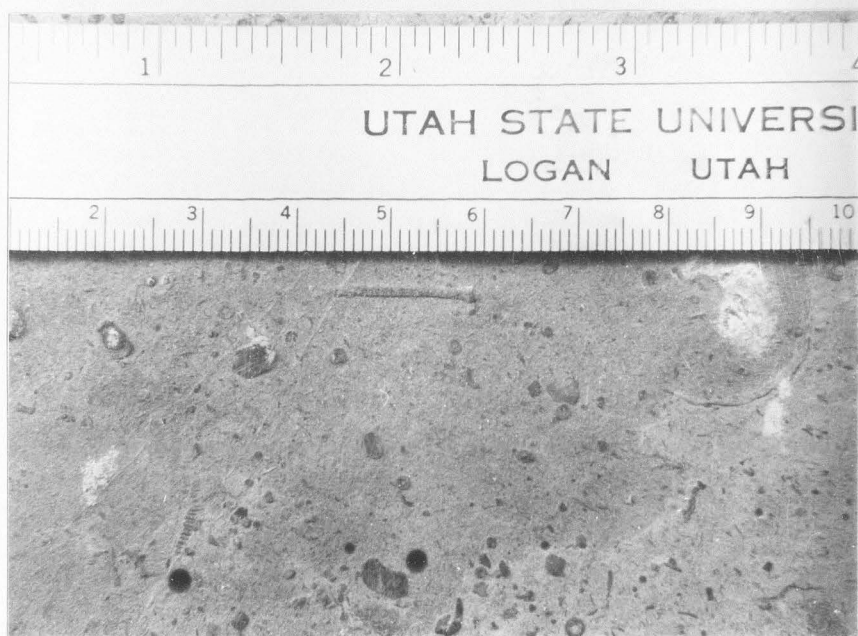


Figure 21. Echinoid spine.

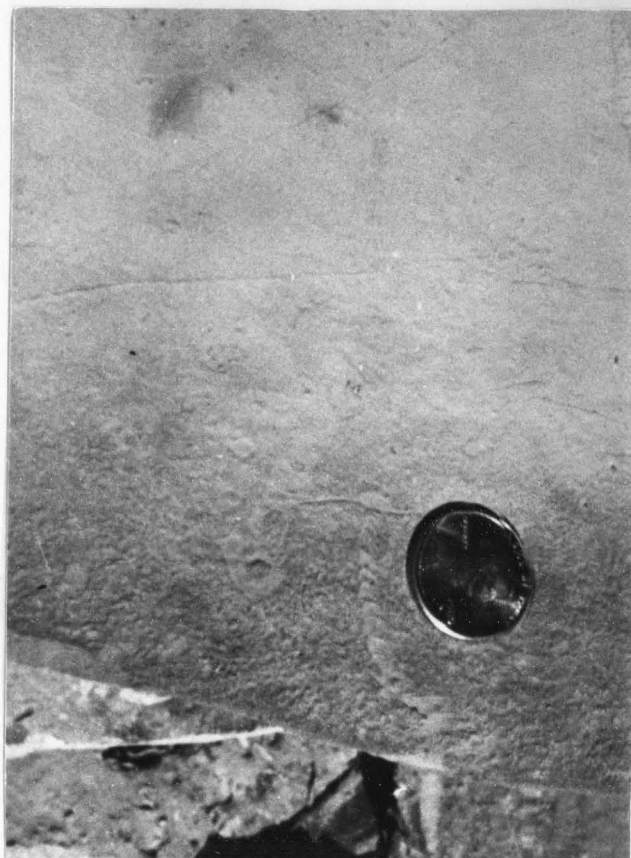


Figure 22. The trace fossil Cruziana.



Figure 23. The trace fossil Zoophycus.



Figure 24. The trace fossil Helminthopsis.

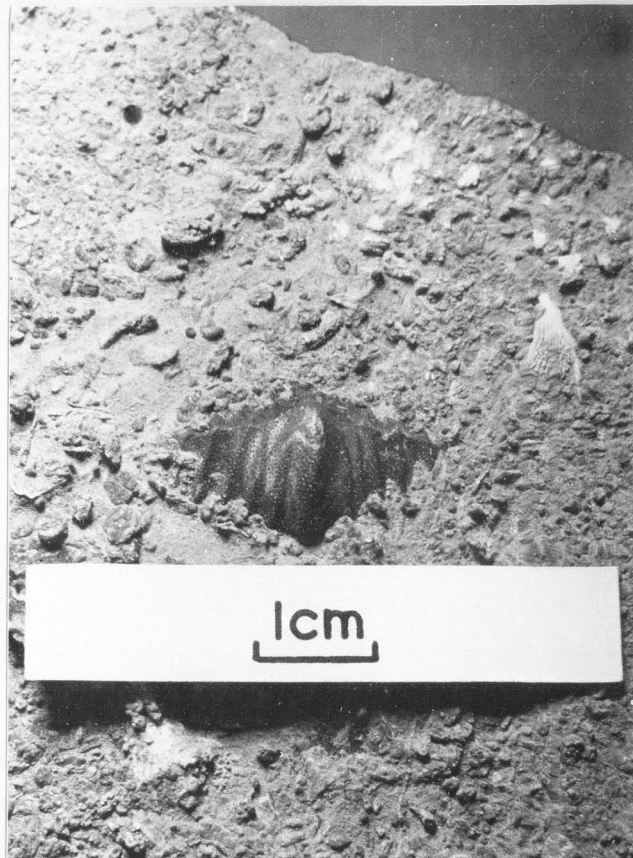


Figure 25. Shark tooth.

noted that well-preserved fossils are generally difficult to find, as they are usually fragmented, silicified, and exfoliated. This deficiency is also true for the study area in this paper. In general, the colonial and solitary rugose corals show the least amount of fragmentation and abrasion. Crinoids were only found as columnals, which were either completely disarticulated or were in short articulated stem segments. Fragmentation of individual columnals was rarely found, and abrasion of individual columnals appeared minimal. Brachiopods were commonly found as unfragmented, articulated individuals often in inferred life position. However, a small percentage of disarticulated valves were also present. Both forms of tabulate corals found in the study area, Aulopora and Syringopora, were dominantly found in the form of fragmented corallites. The gastropod Euomphalus was found only as outlines on the bedding surface, with whole specimens being found only in the float.

Most of the fragmentation which occurred in the taxa present appeared to be the result of weathering of fossils from the strata or the present outcrop, rather than current action acting on the skeletons before burial.

As a measure of the amount of disarticulation and fragmentation which occurred, each bedding surface is placed in one of four categories, each of which is defined in terms of the type of crinoid deposit which was found on it (Appendix). Each category is defined as follows:

Type A deposits: Crinoid columnals are disarticulated, and are clustered in depressions on a scoured surface.

Type B deposits: Crinoid columnals are disarticulated, and are scattered evenly over the entire bedding surface.

Type C deposits: Crinoid columnals are present in short articulated segments.

Type D deposits: The bedding surface is covered by a fine-grained unidentifiable fossil hash.

Orientation Analysis

To provide the basis for inferences concerning paleocurrent direction and intensity, orientation measurements were made on 211 fossils from 29 bedding surfaces located throughout the studied section. Measurements were made on the solitary rugose coral Zaphrentis with a hand compass.

Orientation measurements from the rugose coral represent the direction from the apical end toward the calical end of the corallum. Rose diagrams were constructed from these data to show the measurements taken from each of the 29 bedding surfaces. A composite diagram showing all 211 measurements was also constructed. The rose diagrams were divided into ten degree intervals, with the number of measurements falling within each of the intervals being plotted as a linear function along the radius. Each plot was tested for goodness of fit applied to circular data through the use of the following test statistic:

$$X^2 = (O-E)^2/E \quad (\text{Reyment, 1971, p. 38})$$

Where O is the observed frequency in a sector, and E is the expected frequency in a sector which is calculated by dividing the total number of observations by the number of sectors. The observations were also entered into a computer program which converted degrees into sine and cosine values and computed the radial deviation.

The rose diagrams and computer results show that the mean vectors ranged from 5° to 356° (clockwise) (Appendix). Resulting test statistics indicate that the fossils on all but two of the twenty-nine bedding surfaces from which orientation measurements were taken show a random distribution. The two beds which show a non-random distribution are beds 19 and 116. The composite diagram shows a mean vector at 247° but also has a random distribution (Fig. 26).

Diversity

Two types of diversity were calculated from the faunal information collected from each of the bedding surfaces examined: richness and dominance diversity. Richness, which is defined by the formula:

$$DT = m / \log N \quad (\text{Stanton, 1979, p. 269})$$

where m is the total number of species and N is the total number of individuals, is a measure of the number of taxa corrected for sample size. Dominance diversity, which is a measure of both richness (number of taxa), and equitability (the measure of how uniformly abundant the taxa are), is calculated by the formula:

$$DE = \sum_{i=1}^m p_i \ln p_i \quad (\text{Stanton, 1979, p. 269})$$

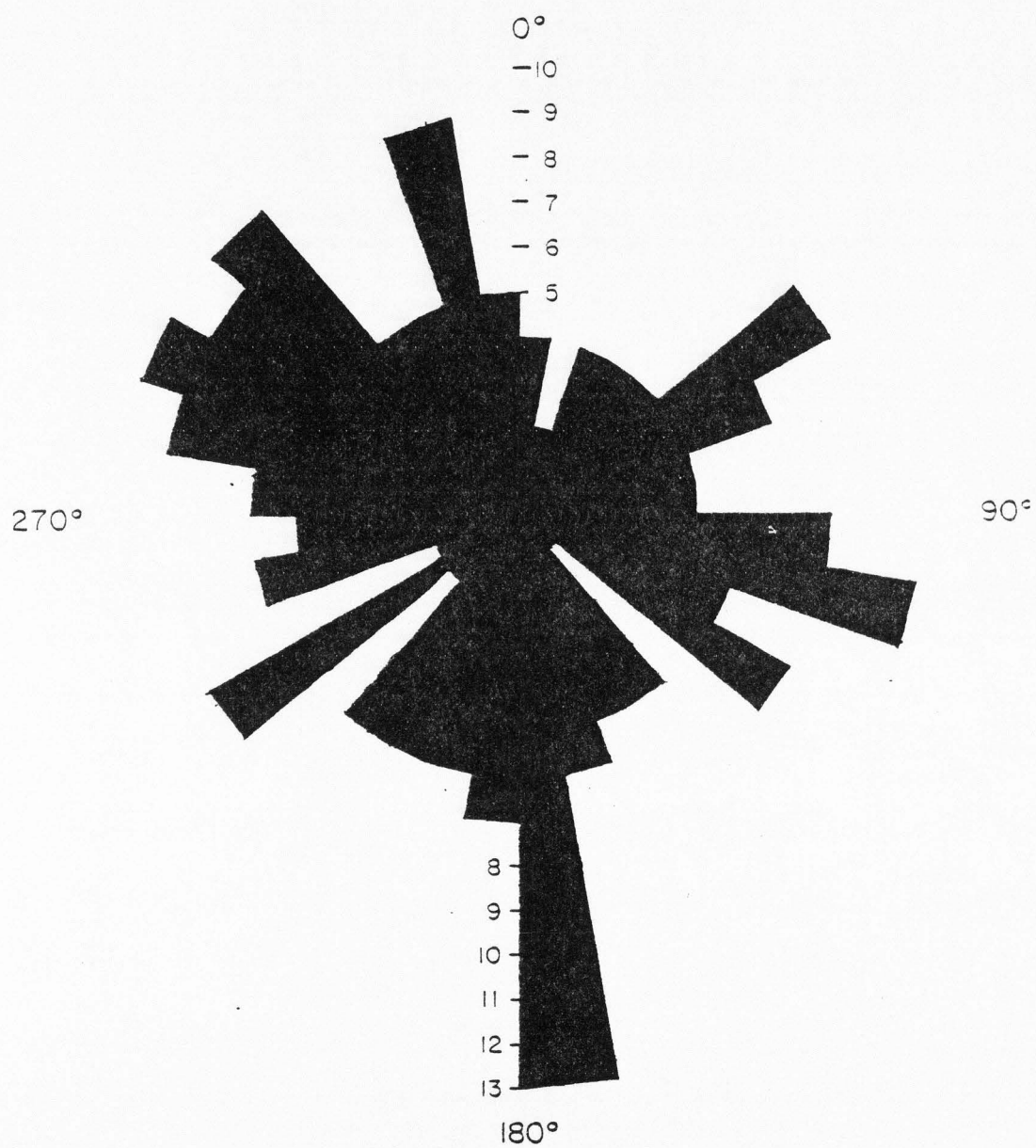


Figure 26. Composite rose diagram of the orientations of the apical ends of 211 solitary rugose corals.

where p_i is the proportion of the i th taxa in the sample.

The number of individuals in each taxon was determined in the following way. For brachiopods, the total number of brachial and pedicle valves were counted. The total number of individuals was then assumed to be equal to the more numerous of the two valves. The number of gastropods was determined by the number of spires present, regardless of whether the whole fossil was present or not. For the tabulate corals, which were found only as fragmented corallites, one individual was assigned to each bedding surface on which the fragments were found, regardless of the number of fragments. The class Echinoidea was represented by the presence of spines. Because very few spines were present on any bedding surface, one individual was assigned to each bed upon which the spines were found. The estimation of the number of individual crinoids and blastoids is made difficult, because each of these two taxa are represented by columnals only. According to Ausich (1980), Lower Mississippian crinoids attained heights between 0 and 100 centimeters above the substrate. Within the Lodgepole at this location, the maximum diameter attained by the columnal is 1.2 centimeters, with a thickness equal to a quarter of the diameter, or 0.3 centimeter. Because columnal diameter is directly correlated with stem length for most crinoid species, the assumption made here is that crinoids with a columnal diameter of 1.2 centimeters attained a stem length of 100 centimeters. Using this extrapolation an approximate upper limit of 330 columnals per individual is obtained by dividing the stem length by the average columnal thickness. The number of Lithostrotionella was based on the

number of coralla present. For the solitary rugose coral Zaphrentis, the number of individuals was determined by the number of apical ends which were counted. The number of sharks present was determined by the presence of teeth. Because the teeth were never numerous, one individual was assigned to each bedding surface on which they were found. For trace fossils, each trace was counted as a single individual.

Results of the calculations show that for richness (DT), values ranged from 0.0 to 7.41, with a mean of 4.12. For dominance diversity (DE), values ranged from 0.0 to 1.95, with a mean of 0.87. Values for each of the bedding surfaces examined may be found in Plate 2.

The values obtained through the use of these two formulas may only give an approximation of the diversity for the communities from which the observed fossil communities are derived. Lawrence (1968) showed that only a small percentage (averaging 30 percent, but as low as 1 percent) of a living community may actually be preserved.

In order to evaluate the effects of differential preservation on diversity, Lasker (1976, p. 85) placed all organisms into three preservational classes:

Class 1--consists of taxa which have readily preserved hard parts.

Class 2--consists of taxa which have hard parts which are easily destroyed.

Class 3--Consists of soft-bodied organisms which are readily preserved.

Three communities, made up of members from each of the three preservational classes in various proportions, were defined. The results of his study showed that communities dominated by a single species from preservational class 1, give rise to fossil communities which would have equability-diversities lower than that of the living communities from which they were derived, because rarer species from preservational class 3 are not preserved. Communities which are over-dominated by a single preservational class would result in fossil communities which have equability-diversities similar to that of the living communities from which they were derived. Communities which are dominated by a single species of preservational class 3 would result in fossil communities with equability-diversities higher than that of the communities from which they were derived, because many dominant soft-bodied organisms would not be preserved.

Calcified Biovolume

The determination of the calcified biovolume for each bedding surface examined involved two processes. In the field, a single morphologic parameter was measured on each fossil counted. These parameters varied from taxon to taxon. On brachiopods the dorsal-ventral length was measured. For solitary rugose corals, the parameter measured was the length along the long axis. The columnal diameter was measured on crinoids and blastoids. For colonial rugose corals, the basal diameter was the parameter measured. On tabulate corals, the parameter measured was the diameter of the individual

corallites, and for the gastropods it was the maximum diameter in the plane of coiling. Secondly, in the laboratory a representative specimen, or model thereof, of each of the taxa found in the study area were immersed in water to determine its volume. In order to determine the calcified biovolume for each bedding surface examined, the following formula was used to relate laboratory and field data on that genus:

$$\begin{array}{l} \text{Calcified Biovolume Estimator of Fossil} = \\ \frac{\begin{array}{l} \text{parameter dimension} \\ \text{of fossil (mm)} \end{array} \times \begin{array}{l} \text{volume of the representative} \\ \text{specimen or model (cm}^3\text{)} \end{array}}{\begin{array}{l} \text{parameter dimension of the representative specimen} \\ \text{of model (mm)} \end{array}} \end{array}$$

The total biovolume present on each bedding surface was then calculated (Plate 2). This representation provides information concerning the approximate carrying capacity of a temporal environment, and will be used as the basis for inferences concerning associated biomass.

Results of this analysis show that the calcified biovolume contained on the bedding surfaces examined ranged from 0.0 to 30,015 cubic centimeters, with a mean value of 744.1 cubic centimeters per bedding surface.

Faunal Association

Another of the objectives is to determine the various faunal associations. The first step in the determination of these associations is the calculation of an index of affinity. This was accomplished through the use of the formula for Fager's similarity

coefficient (Sf) (Fager and McGowen, 1963, p. 454) which is as follows:

$$Sf = \frac{C}{\sqrt{N_1 N_2}} - \frac{1}{\sqrt{2} N_2}$$

where C is the number of occurrences of taxa N_1 and N_2 together, N_1 is the total number of occurrences of taxon N_1 , and N_2 is the total number of occurrences of taxon N_2 , where N_1 is greater than N_2 . Because these similarity coefficients may be either positive or negative, the absolute value of the smallest negative value was added to the other values in order that all the values may be positive. To generate a dendrogram these values were then subtracted from 1.5, so that the closer a value is to zero, the closer the association between the taxa being compared.

The next step in the determination of faunal associations is the clustering of the values calculated by the above procedure. The method of clustering used was the unweighted pair-group method using arithmetic averages (UPGMA). For an explanation of this method, see Sokal and Sneath (1963, pp. 216-240). For the purpose of interpreting the resulting dendrogram, clusters which links at values of 1.00 or less are considered to represent a significant association.

Three faunal associations are indicated by this method (Fig. 27). These associations are as follows:

Association 1: Zaphrentis-Crinoid-Syringopora-Euomphalus-Echinoid-Cleiothyridinia-Unispirifer-Spirifer-Orthotetes-Lithostrotionella-Flexaria-Camarotoechia-Schizophonia

Association 2: Cruziana-Dwelling Tube

Association 3: Shark-Blastoid-Helminthopsis

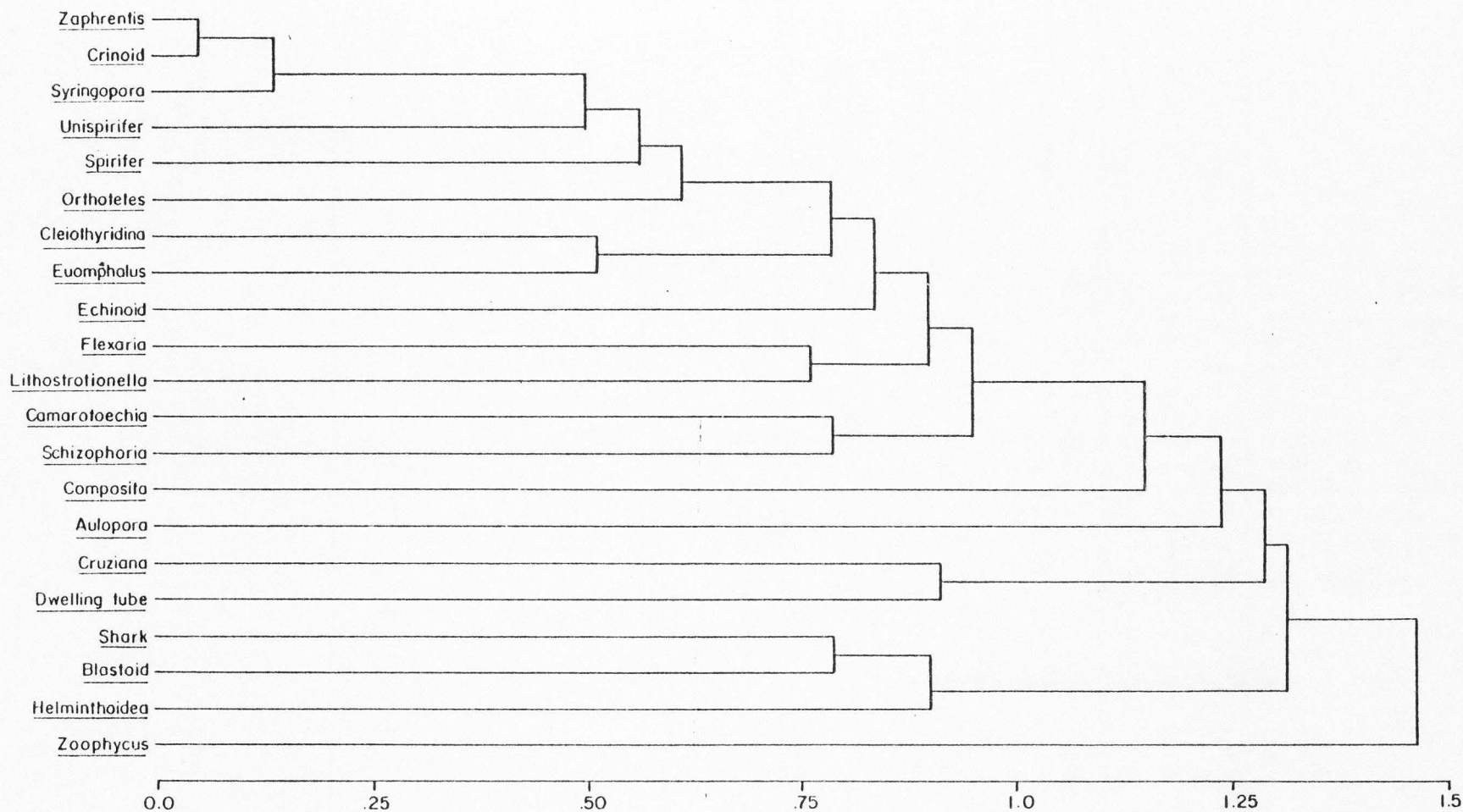


Figure 27. Dendrogram of faunal associations of the Lodgepole Formation, by unweighted pair-group method using arithmetic averages.

As a result of strong affinities within Association 1, several "sub-associations" are recognized. These sub-associations include:

Sub-association a: Zaphrentis-Crinoid-Syringopora-Spirifer-Orthotetes

Sub-association b: Cleiothyridina-Euomphalus

Sub-association c: Flexaria-Lithostrotionella

Sub-association d: Camarotoechia-Schizophoria

Johnson (1972, p. 151), stated that "... in pair by pair analysis, it is often possible to assemble groups of significantly associated or correlated species (species A is significantly associated with species B, and both with species C, etc.). However, groups of species defined in this manner may not actually occur together very often in nature." To see if this were true for any of the above associations, a limiting member (the taxon in an association which was found on the least number of bedding surfaces) was designated. It was then determined how often the other members of an association coexisted with the limiting member. In faunal Association 1, the brachiopod Camarotoechia is the limiting member, found on 3 of the 125 bedding surfaces examined. In all three beds where Camarotoechia was found, a minimum of five members of association 1 are also present. In faunal Association 2, the dwelling tubes are the limiting member, found on only one bedding surface. The trace fossil Cruziana is the other member of this association, and is found on the same bedding surface as the dwelling tubes. The limiting member of Association 3 are blastoids, which occur on 1 of the 125 bedding surfaces. All of the other members of this association are also found to occur on this bedding surface.

Trophic Structure

In most traditional studies dealing with feeding interrelationships among various organisms, the concept of a food chain has been emphasized. However, problems arise when trying to apply this concept to ancient communities, because the predators and the primary producers are rarely preserved. Based on work done with modern boreal and arctic marine communities, E. P. Turpaeva (1948, published in the U.S. in 1957), developed an approach to the study of trophic groups which is much more easily applied to fossil communities. In this approach five trophic groups are recognized. These are defined as follows (Walker, 1972, p. 83):

1. Swallowers (infaunal deposit feeders)--feed within the bottom sediment.
2. Collectors (epifaunal deposit feeders, some scavengers, and browsing herbivores)--collect detritus from the sediment surface.
3. Filterers-A (low-level suspension feeders)--filter food from immediately above the bottom.
4. Filterers-B (high-level suspension feeders)--filters food from water some distance above the bottom.
5. Awaiters (passive suspension feeders??)--traps food from a current of water some distance above the bottom.

For the purpose of this study Turpaeva's "Filterer" categories were further subdivided, so that eight trophic groups are recognized:

1. Very high-level filter feeders (VHF)
2. High-level filter feeders (HF)

3. Intermediate-level filter feeders (IF)
4. Low-level filter feeders (LF)
5. Very low-level filter feeders (VLF)
6. Infaunal filter feeders (SF)
7. Mobile epi- or endobenthonic deposit feeders (MED)
8. Nektic carnivores (NC).

Assignment of each of the taxa to one of these trophic groups is based on the work of Yonge (1954), which was later corrected and modified by Walker and Bambach (1974), who assigned feeding mechanisms to common fossil taxa (Fig. 28). A bed-by-bed presentation of the taxa present and the trophic group to which each belongs, is given in Plate 2.

Through the application of this method of studying trophic groups, Turpaeva recognized several relationships (Walker, 1972, p. 83):

1. A community is usually dominated by one trophic group.
2. If the most dominant species (in terms of biomass) in the community belongs to one particular trophic group, the next most abundant species belongs to a different group. Often, the third most dominant species belongs to still a third trophic group. Thus, to quote Turpaeva (1957, p. 144), "the dominant group of species in a biocoenosis consists of representatives of different food groups."
3. Among the various species of a community which belong to a given trophic group, a single species commonly dominates the group in terms of biomass.
4. Thus, the several most dominant species in the benthic
















































		MAIN FEEDING TYPE IN GROUP 				SUBSIDIARY FEEDING TYPE IN GROUP 					
TAXON		SMALL PARTICLES				LARGE PARTICLES				FLUIDS	
		PSEUDO- PODIAL	CILIARY & FLAGELL.*	MUCUS	TENTACU- LATE & SETOUS*	SEDIMENT SWALLOW- ING	SCRAPE & BORE	SEIZING			
								& SWALLOW- ING	& CHEW- ING	& EXTERNAL DIGESTION	
* COMMON AS FOSSILS											
PROTOZOA*											
PORIFERA*											
COELEN- T.	HYDROZOA							NEMATOC.			
	SCYPHOZOA							NEMATOC.			
	ANTHOZOA*							NEMATOC.			
PLATYHELMINTHES											
NEMATODA											
BRYOZOA*											
BRACHIOPODA*											
MOL- LUSCA	AMPHINEURA										
	GASTROPODA*			VERMETID			RADULA				
	BIVALVIA*		CTENID.		PROTOBR.			SEPTIBR.			
	SCAPHOPODA										
	CEPHALOPODA*										
ANNELIDA*(BUR.)			TENTAC.	POLYCH.	POLYCH.						
ARTHRO- PO- DA	CRUSTACEA*										
	ARACHNIDA										
	INSECTA										
ECHINODERMATA	CRINOIDEA*		AMBULAC.								
	ASTEROIDEA										
	OPHIUROIDEA										
	ECHINOIDEA*										
	HOLOTHUROID.										
HEMICHORDATA*											
TUNICATA											
CEPHALOCHORDATA											

Figure 28. Feeding mechanisms in invertebrate animals (from Walker and Bambach, 1974).

community use the available food resources more fully than if they fed at a single level, and competition for food is minimized.

Turpaeva's trophic group model is not without its limitations. The first of these limitations is that vertical stratification in the height above the substrate at which each member of a community feeds is not the only way in which food resources may be divided, and thereby limit competition for food. If the density of the filter feeders in a community is kept low, competition for food may not be necessary. Lang (1971) observed that aggression occurs between many species of corals, with one coral killing the tissue of other corals which may have settled within the reach of its tentacles. This particular aggression may be a means by which community density is kept low, thus insuring an adequate food supply for each individual. However, since what is killed is the fleshy tissue, direct evidence of this type of aggression is rarely preserved in the fossil record. Within the study section, the preserved remains of the individuals are commonly found in small clusters on the bedding surface, with the areas around these clusters being barren. This suggests that within these clusters, factors which would control density were not very active.

Another way in which feeding competition may be minimized is by the physical constraints on the size of the food particle that an individual can ingest. According to Walker and Bambach (1974) the size range of the particle that an individual can ingest depends on two factors: the size of the individual, and the operation of its

feeding mechanisms. Again, evidence of how an organism fed, or the size of the food particle which it could ingest, is rarely preserved.

A second limitation of Turpaeva's model is that when the individuals of a community are assigned to a trophic group, it is assumed that all the individuals are at the same stage of growth (generally the adult stage). This assumption is at best only an approximation of the true situation. During the invasion of a clean, barren substrate, all sessile filter-feeding juveniles initially feed at approximately the same level. Differentiation in the feeding levels occurred as the individuals mature.

Within a well established, stable community new individuals are continually being added which frequently begin life in a trophic group which is different from that it will occupy as an adult. So that for each taxon a continuum may exist between the trophic group occupied by its juveniles and the trophic groups occupied by its adults.

In the two preceding examples, individuals start life in a low-level filter-feeding trophic group and as they become adults they occupy successively higher-level filter-feeding trophic groups. The opposite case may also occur in nature. One of the taxa identified within the Lodgepole at this location is the brachiopod Orthotetes. As a juvenile, Orthotetes lives umbonally cemented to various hard substrates. But as an adult, Orthotetes frequently was broken loose from its substrate and toppled or settled into a very low-level filter feeding mode of life. If this initial surface of attachment happened to be a crinoid, the juvenile may have fed at a very

high-level before becoming a very low-level filter feeder as an adult.

A third limitation to Turpaeva's model is the idea that the food utilized by filter feeding organisms is not a limiting resource. Levinton (1972, p. 475) stated that:

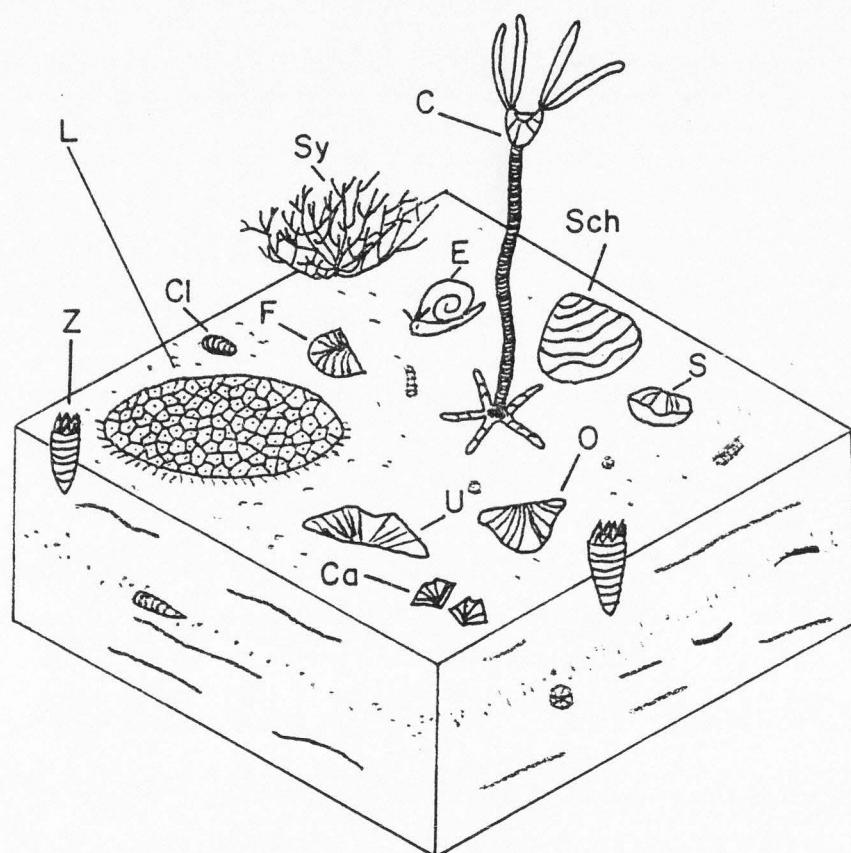
Suspension-feeding benthic animals feed on a passing current of water. It strains particles or creates a current directed toward a straining organ. Some particles are too large to be drawn in. Particles drawn in are either ingested or rejected as pseudo-feces. Ingested particles may pass through the gut without being digested. When one organism is unsuccessful at digesting it, the undigested particle will be carried away some distance, depending upon current velocity. If no two closely located individuals of the same suspension-feeding species or of different species have access to the same food particles, one species population might thrive under certain food conditions but not at the expense of any other species. Each individual's food is, in effect, unique. Under this condition, different suspension-feeding species in a small area would not be exploiting the same resource. Therefore, competitive exclusion by exploitation could not take place in suspension-feeding populations. In addition, since all individuals would be independent, trophic structure, that is a set of species in the same community with contiguous niches, would not evolve.

While this condition may be true for the shallow water communities examined by Levinton, the food utilized by filter feeding organisms varies in both quantity and quality with depth. Through the examination of the gut contents from brachiopods and bivalves, Suchanek and Levinton (1974) found that phytoplankton (a primary food source for filter feeders) became more scarce with depth, both in number of individuals and in number of genera. From this it appears that Turpaeva's model is more applicable to deeper water situations.

Application of Turpaeva's model to the faunal associations determined in the previous section appears to support those

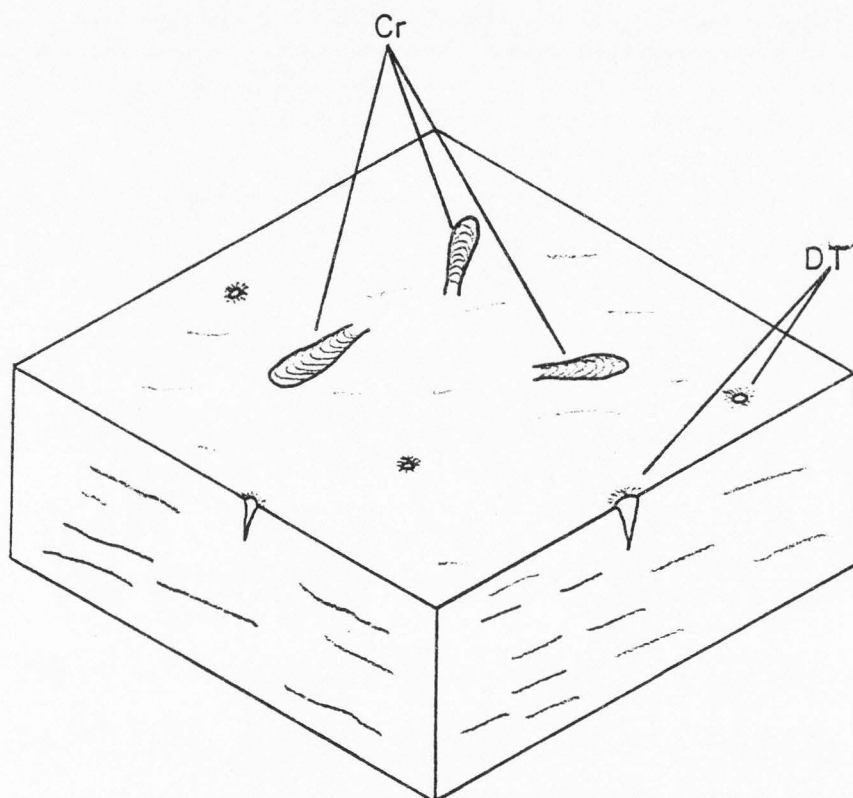
relationships summarized by Walker (1972, p. 83). Faunal Association 1, which is composed of Zaphrentis, Lithostrotionella, Syringopora, Crinoids, Echinoids, Euomphalus, Unispirifer, Spirifer, Orthotetes, Cleiothyridina, Flexaria, Camarotoechia, and Schizophoria, consists of both filter feeders and epi- and endobenthonic deposit feeders (Fig. 29). Within the filter feeders of this association, a distinct stratification can be seen in the height above the sediment-water interface at which each feeds, with one very high-level filter feeder, two high-level filter feeders, four intermediate-level filter feeders, two low-level filter feeders, and two very low-level filter feeders. Faunal Association 2 is represented by two trace fossils, Cruziana and dwelling tubes (Fig. 30). According to Osgood (1975), Cruziana is thought to be the crawling traces of a half-buried trilobite, and therefore would represent an epi- or endobenthonic deposit feeder. The dwelling tube, unlike Cruziana cannot be placed into a trophic group, as it only represents a dwelling place and gives no information as to how the organism which occupied it procured food. Faunal Association 3 represents three trophic groups, with sharks representing nektonic carnivores, blastoids representing very high-level filter feeders and Helminthopsis representing epi- or endobenthonic deposit feeders (Fig. 31).

Thus, it appears that the faunal associations reconstructed for the Lodgepole Formation are the result of two factors. The first of these factors is the tendency towards a vertical stratification of the various members of the associations. This, according to Walker and Bambach (1974), provides a method for subdividing food resources,



- | | |
|------------------|-----------------------|
| C - Crinoid | Cl - Cleiothyridina |
| Sy - Syringopora | Sch - Schizophoria |
| Z - Zaphrentis | F - Flexaria |
| E - Euomphalus | O - Orthotetes |
| U - Unispirifer | Ca - Camarotoechia |
| S - Spirifer | L - Lithostrotionella |

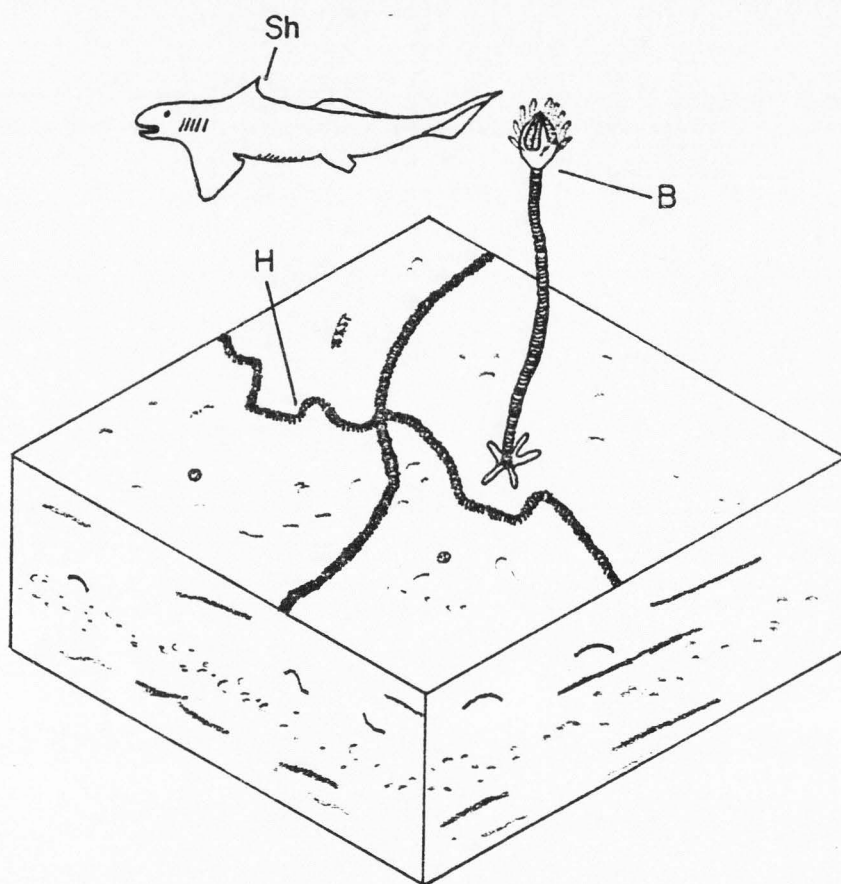
Figure 29. Block diagram of Faunal Association 1.



DT- Dwelling Tubes

Cr- Cruziana

Figure 30. Block Diagram of Faunal Association 2.



B - Blastoid
S - Shark
H - Helminthopsis

Figure 31. Block Diagram of Faunal Association 3.

and permits a diversity of feeding relationships even though the variety of food may be limited. Of equal importance in determining faunal associations is the second factor, that of direct biological interaction between members of an association, such as predator-prey relationships. This type of relationship may have been important in the development of Faunal Association 3. Moy-Thomas and Miles (1971) have indicated that the stomach content of modern shell-crushing sharks included brachiopod fragments, crinoids, foraminifera, and large crabs.

PALEOECOLOGY OF FOSSIL ASSEMBLAGES

Paleocurrents-Intensity and Direction

Study of orientational data, crinoid deposits, and insoluble residue content of the early Mississippian Lodgepole Formation of southeastern Idaho suggest that, at the time of deposition, current action was weak. Data upon which the following discussion is based have been presented in previous sections of this study.

Brenchly and Newell (1970, p. 218) stated that "... if fossil unidirectional orientations occur in transported assemblages, then a position with the center of gravity into the current is perhaps most likely." Due to a hollow calyx, the center of gravity of solitary rugose corals is located nearer to the apical end, and therefore, in a unidirectional current should orient in such a way that the calyx is pointing downstream. This orientation is confirmed by flume experiments involving both idealized models and actual horn corals. In an experiment designed to study the effects of a unidirectional current on models of various shapes, Abbott (1974, p. 10) found that right-angle cones would orient "... so that their apexes pointed upstream." Similar results were obtained by Sweide (1977), when models of solitary rugose corals were subjected to unidirectional currents.

Applying the above to the orientational data previously presented (Appendix, and Fig. 26), the solitary rugose corals

within the Lodgepole at this location are found to be oriented randomly. This suggests that unidirectional currents strong enough to orient these corals were not present during the period of time between their death and their burial or that multidirectional currents of similar competency operated over the substrate. Alternatively, browsers, scavengers, and sediment miners may have disoriented the skeleton.

The examination of the various types of crinoid deposits present in the study area also provides evidence which supports the conclusion of relatively weak bottom currents.

"The specific geometry developed in a deposit that contains abundant crinoid debris is thought to be most importantly controlled by two factors, the rate of sedimentation and the strength of the bottom currents" (Lane, 1971, p. 1439-1440). Lane further implied that the rate of sedimentation and current strength are directly related to the degree to which the crinoid skeleton is broken up after death, but before burial. Relatively intact skeletons represent a high sedimentation rate and/or weak bottom currents (Fig. 32).

The four types of crinoidal deposits found in the study area (see p. 47) seem to be the result of the following current and sedimentation regimes. Type A deposits, which are similar to Lane's "Debris Lense," consist of disarticulated crinoid columnals which are confined to depressions in a scoured surface. This type of deposit is the result of an environment in which there is a low sedimentation rate and/or rather strong bottom currents. Type B deposits contain crinoids which are completely disarticulated and

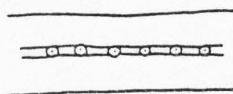
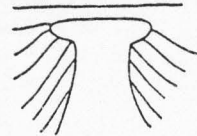
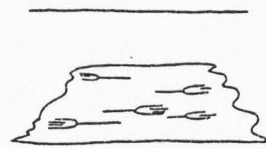

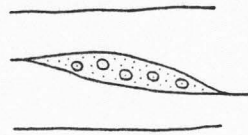
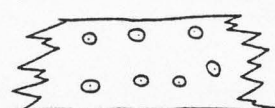
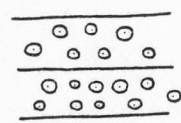
TYPES OF CRINOIDAL DEPOSITS			
SEDIMENTATION RATE	CURRENTS	SEDIMENTS	
		TERRIGENEOUS	CARBONATE
HIGH	STRONG	Thin stringers of crinoidal debris 	Reef dwellers  Racine Dolomite
HIGH		 Crawfordsville	Crinoid nests  Hampton Fm.
LOW	WEAK	Non - deposition or erosion	Debris lenses  St. Joe Ls.
LOW		 Stobo lense	Crinoidal limestone  Burlington Ls.

Figure 32. Generalized model of different types of sedimentary deposits rich in crinoids (from Lane, 1971, p. 1439).

the columnals are scattered evenly over the bedding surface. This type of deposit corresponds to Lane's "Crinoidal Limestone," and indicates deposition under the influence of weak bottom currents and/or low sedimentation rates. The third type of crinoid deposit found in the study area, Type C deposits, have no direct equivalent in Lane's (1971) model. It is, however, somewhat similar to Lane's "Crinoidal Nests," in that most of the crinoid columnals are found in short, articulated segments, which suggests deposition in an environment with a higher sedimentation rate and/or weaker bottom currents relative to Type B deposits. Type D deposits consist of extremely fine-grained fossil hash which is distributed evenly over the entire bedding surface. Whereas crinoidal debris may not be present in these deposits, other fossils form a fine-grained hash. If the same criteria as used above for determining the sedimentation rate and current intensity are used, deposition under conditions of low sedimentation rates and/or strong bottom currents is indicated for beds that are characterized as Type D deposits.

In applying the above classification, it is found that 106 of the 125 bedding surfaces (84.8%) contain Type B or Type C deposits, 6 of the 125 bedding surfaces (4.8%) contain Type A or D deposits and the remaining 13 bedding surfaces (10.4%) contain faunas which do not contain crinoid debris. As with the orientational data, crinoid deposits indicates that the majority of the beds of the Lodgepole Formation were deposited in an environment in which current intensities were relatively weak.

Assuming that high amounts (weight percent) of insoluble

residue indicate quiet water conditions, i.e., out of areas of intense wave and current action which would keep terrigenous material in suspension, the results from the insoluble residual analyses (Plate 1) do not support the conclusion reached from the orientational data and from the crinoid deposits. In all instances the insoluble residue content (weight percent) of each bed examined was below 9.5%, which suggests that some current action may have been present to keep terrigenously derived insoluble material in suspension. This lack of insoluble material may, however, be explained in terms of supply. If this area at the time of deposition of the Lodgepole was adjacent to a very low-lying landmass or was located at some distance from a source area for terrigenous insoluble material, the amount of such material being supplied to the site of deposition would be low. Paleogeographic reconstructions of this area for the early Mississippian (Gutschick, Sandberg and Sando, 1980; Sando, 1976; Rose, 1976) suggest that such may be the case, because these reconstructions place this area to the west of a wide, well-defined carbonate platform.

Sedimentation Rate

Examination of the insoluble residue content, crinoidal deposits and coral growth forms at the location of this study suggests that during Lodgepole deposition, the sedimentation rate was relatively low.

Results from the insoluble residue analysis are used here as a measure of terrigenous influx, wherein a high insoluble residue content indicates a high rate of influx of terrigenous material.

Plate 1 shows that the maximum content of insoluble material present within a single sample is 9.5%. This indicates that the rate of terrigenous influx was relatively low. A second possible explanation for the low amounts of insoluble residue, is the dilution of the terrigenous material by relatively higher amounts of carbonate.

This conclusion is supported by the types of crinoid deposits present throughout the studied section. As indicated in the paleo-current section, the type of crinoid deposit may also be used as an indicator of the sedimentation rate. Lane (1971) indicated that environments with high sedimentation rates and/or weak bottom currents tend to produce deposits in which individual crinoids remain articulated, whereas deposits which form in environments in which the sedimentation rates are low and/or the bottom currents are strong tend to be composed of disarticulated and fragmented crinoid skeletons. Appendix shows that the majority (84.8%) of the bedding surfaces examined contained Type B deposits (30.4%), which suggest low sedimentation rates and/or weak bottom currents, or Type C deposits (54.4%) which suggest a sedimentation rate relatively higher than that for Type B deposits and/or weaker bottom currents. As Type C deposits consist only of short, articulated stem segments rather than complete, intact crinoid skeletons, they suggest a sedimentation rate that was slightly higher than that for Type B deposits, but one which was still generally low.

In addition to insoluble content and crinoidal deposits, coral growth forms were examined as indicators of the sedimentation rate. The coralla examined belong to the genus Lithostrotionella, and

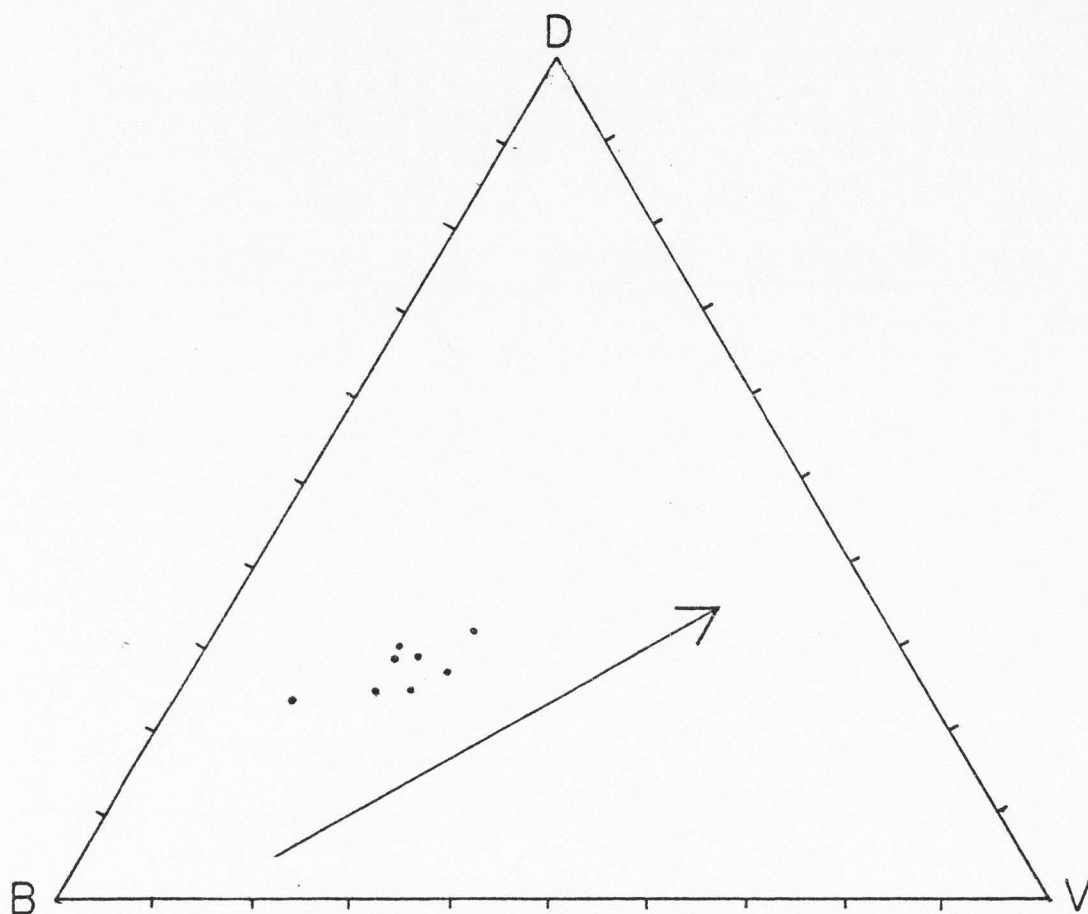
were found both in-place and as weathered-free fossils in talus derived from the Lodgepole. Three parameters were measured from eight coralla: the diameter of the basal resting surface; the maximum vertical distance (height) measured perpendicular to the base, and the length of a diagonal which extends from the center of the resting base to the growth surface, at an angle of approximately 45° to the base. These parameters were then plotted on a triangular diagram (Fig. 33).

In general, the coralla of Lithostrotionella are dome-shaped and to have flat basal resting surfaces. According to Philcox (1971), the shape of the non-growth surfaces (either the base or the sides of the colony) is controlled by the sedimentation rate. Philcox further stated that a flat-based corallum would only result under conditions of extremely low sedimentation rates. Increased sedimentation rates would cause the non-growth surfaces to become conical, with coralla ultimately assuming a cylindrical shape when the sedimentation rate equalled the maximum growth rate of the coral (Fig. 34). Hubbard (1974) found that a similar relationship between growth form and sedimentation rate can be seen today in modern coral colonies.

Therefore, like the insoluble content and crinoid deposits, the dominant coral growth-form also suggests low sedimentation rates at the time of Lodgepole deposition.

Bathymetric Reconstruction

In trying to reconstruct the bathymetry of the depositional site



B-basal diameter

V-vertical length (height)

D-diagonal length

Figure 33. Graphical representation of *Lithostrotionella* coralla. Arrow indicates trend in corallum shape with an increasing sedimentation rate.

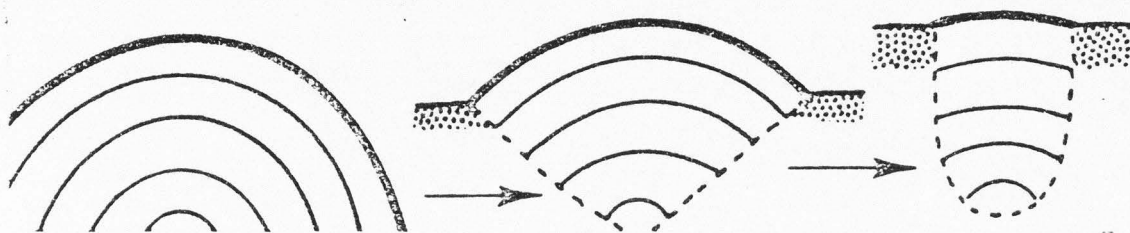


Figure 34. Summary of the effects of increasing sedimentation rate on the growth form of radial favositids (Philcox, 1971).

of the Lodgepole at this location, several lines of evidence which give only a wide depth range had to be used, as no single line of evidence which would give an absolute depth was found.

The minimum depth for this bathymetric reconstruction is indicated by sedimentary structures which are present and those that are not present. Fine laminations, from one to several millimeters thick, characterize the limestones of the Lodgepole within this study section. These structures together with the lack of such features as ooids, ripple marks, and mudcracks suggest that deposition took place under fairly quiet conditions below effective wave base. According to Emery (1966), for the East Coast of the United States this depth may be as much as 200 meters during storms, but it is generally around 20 meters. However, these depths would represent maximum depths for the effective wave base of this location during the Mississippian, as the basin in which deposition was taking place is smaller in terms of surface area than the Atlantic Ocean.

Trace fossils support the conclusion of deposition below wave base. According to Frey (1975), based on the work of Seilacher (1964), two trace fossils which were found in the study section may be used as indicators of the benthic environments, which in turn generally relate to energy levels. Cruziana is found from shallow littoral depths, generally below daily wave base but not below storm wave base, to slightly quieter offshore conditions. Zoophycus is found from sublittoral to bathyal depths, and may overlap the range of Cruziana.

Inferences concerning the maximum depth at the time of

deposition are based on two factors: the presence of light, and the presence of oxygen. The lack of algally produced features such as stromatolites and algal laminations suggests that water depth exceeded the depth to which light was able to penetrate, or else that grazing predators were abundant and efficient. According to Schopf (1980), photosynthesis is generally limited to depths shallower than 100 meters, but may take place in depths up to 200 meters.

The presence of organisms such as crinoids (Clark, 1957) and corals (Wells, 1957), which require well-oxygenated conditions, indicates that the maximum water depth at the time of deposition had to have been above the zone of oxygen depletion. According to Schopf (1980), this zone exists at depths of between 0.5 and 2 kilometers in the oceans today.

Wilson (1975) proposed a sequence of facies belts based on wave base, oxygen levels, rock type and primary sedimentary structures present within each of these belts (Fig. 35). From Plate 1, it can be seen that the rocks within the study area consist primarily of fossiliferous wackestones, mudstones, and packstones, which are either structureless or have thin, parallel laminae. From the discussion of the preceding paragraphs, it has been concluded that deposition took place below normal effective wave base, but above the oxygen minimum. Using this information and Wilson's (1975, p. 26) model, it is likely that deposition took place in what Wilson termed the "Shelf Facies." Wilson (1975, p. 355) described this belt in the following way: "The water is tens of meters or even a hundred meters

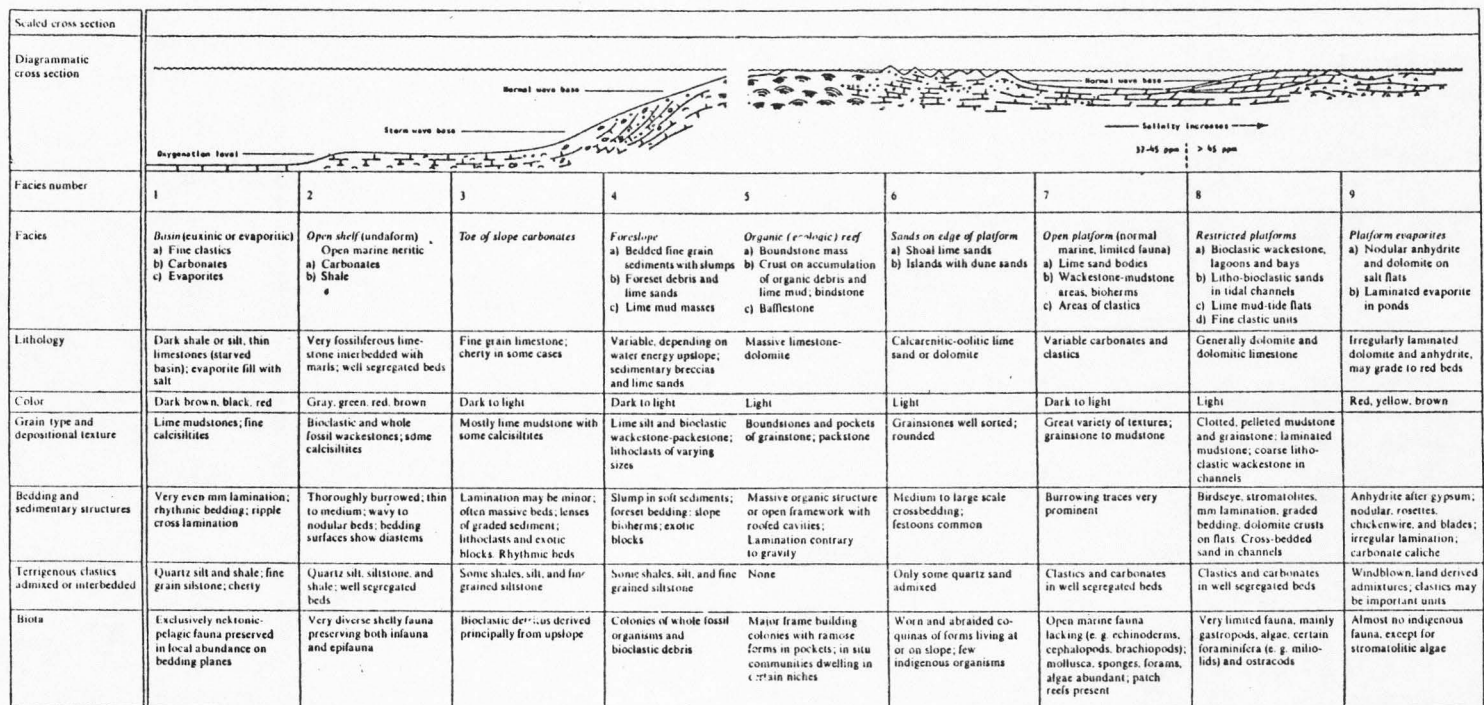


Figure 35. Idealized sequence of Standard Facies Belts (from Wilson, 1975, pp. 26-27).

deep, generally oxygenated and of normal salinity, with good current circulation. The depth is sufficient to be below normal wave base, but intermittent storms affect bottom sediment." Wilson also indicated that the grain types and depositional textures consist of bioclastic and whole fossil wackestone, with occasional beds of bioclastic grainstones and some calcisiltite.

Substrate

The dominant substrate, during the deposition of rocks within this study section, is inferred to have been one of carbonate mud. Evidence which suggests this conclusion is the mud supported nature of the rocks and the low content of insoluble residue, which was found never to exceed 9.5 percent of the rocks by weight. Reducing conditions are also believed to have existed during or shortly after the time of deposition. Evidence for this is the dark color of the rocks, which ranges from medium light gray (N6) to dark gray (N3), and by the organic content, which ranges from 0.05 percent to 1.07 percent of the rock by weight. The $Eh=0$ line is thought to have been located just below the sediment-water interface. This assumption is based on the presence of very-low-level filter feeders throughout the study section, and on the infrequency of burrowing traces suggesting the presence of some barrier which prevented the development of a vagile infauna.

COMMUNITY SUCCESSION

Stages of Succession

Study of the fauna on bedding surfaces directly above bedding surfaces which were barren or which contained a fine-grained unidentifiable fossil hash suggests that four successional episodes or stages can be reconstructed. Throughout the majority of the study section, the successional sequence involves only the first three of these stages. These stages are as follows:

1. Following a perturbation (physical or biological) which left the substratum essentially barren, the surface was inhabited by various members of the stage 1 fauna, which include: Orthotetes, Unispirifer, Spirifer, Schizophoria, Echinoids, Crinoids, Euomphalus, and Helminthopsis (Fig. 36).

Of these taxa only Helminthopsis can be considered a characteristic species, i.e., those species that occur more often and in the greatest number in a particular environment (Johnson, 1972) for this stage. The remaining taxa have the characteristics of ubiquitous species, in that they are found in several stages (environments), but are not characteristic of any one. According to Walker and Alberstadt (1975), early stages of succession, i.e., pioneer stages, are characterized by the presence of taxa which are ubiquitous.

2. Succession continued with the addition of several new taxa and the loss of the trace fossil Helminthopsis. New taxa added

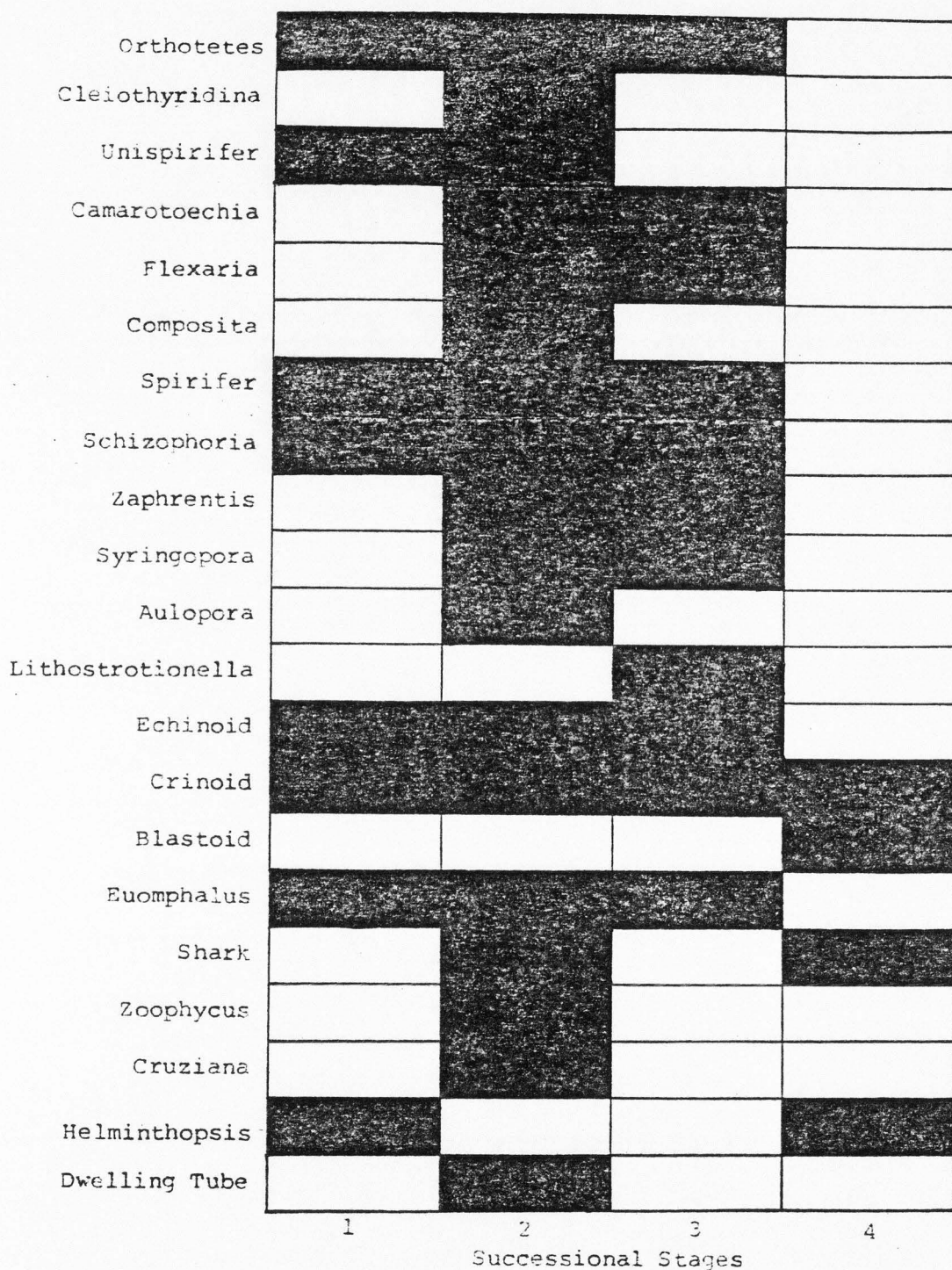


Figure 36. Faunal composition of the various successional stages.

include: Cleiothyridina, Camarotoechia, Flexaria, Composita, Zaphrentis, Syringopora, Aulopora, shark, Zoophycus, Cruziana, and dwelling tubes (Fig. 36).

Of these, Cleiothyridina, Composita, Aulopora, Zoophycus, Cruziana, and dwelling tubes are found only in this stage of succession, and therefore represent characteristic species.

3. Stage 3, the final stage of this successional sequence is represented by the addition of Lithostrotionella and the loss of several taxa, which include Cleiothyridina, Composita, Aulopora, Zoophycus, Unispirifer, shark, Cruziana, and dwelling tubes (Fig. 36).

The fourth successional episode is represented by crinoids, blastoids, shark, and the trace fossil Helminthopsis. Its placement into the successional sequence is uncertain, as it was found on only one bedding surface. This bedding surface is located at the contact between the Lodgepole Formation and the overlying sandstones and siltstones of the Humbug Formation, suggesting that successional stage 4 is represented by a fauna that adjusted to environmental conditions that were never present during the deposition of the rest of the Lodgepole Formation of the study section.

Evaluation of Autogenic and Allogenic Succession and Regression

In order to evaluate the concepts of autogenic and allogenic succession, all possible combinations of change in successional stages with change, or lack of change in rock type, from bed to bed, must be examined. Three combinations are considered significant to

this study. These include:

1. Change in the successional stage with a change in the rock type.
2. Change in the successional stage without a change in rock type.
3. Change in the rock type without a change in the successional stage.

Combination 1 was observed to have occurred ten times within the study section. Change in successional stage with a change in rock type is considered to represent allogenic succession. While general environmental conditions (bathymetry, sedimentation rate, current intensity, and substrate) have been described, the different rock types represent variations in these general conditions, with packstones indicating higher energy conditions, mudstones indicating lower energy conditions, and wackestones indicating energy conditions intermediate between those of packstones and mudstones. Changes in the successional stages which were observed to take place include: Stage 1 advancing to stage 2; stage 2 advancing to stage 3; a barren bedding surface advancing to stage 2; and stage 1 advancing to stage 4.

Combination 2 was observed to have occurred sixteen times within the study section. Change in the successional stage without a change in the rock type is considered to represent autogenic succession. Combination 2 illustrates that changes in the physical environment may not have been necessary to cause a change in the successional stage. Observed changes in the successional stages include: barren bedding surfaces advancing to stage 1; stage 1

advancing to stage 2; barren bedding surfaces advancing to stage 2; and stage 1 advancing to stage 3.

Combination 3, which was observed to occur eighteen times within the study section, is also thought to indicate autogenic succession. Change in rock type without a change in the successional stage suggests that the successional stage is independent of the environmental changes indicated by the different rock types, or that the intensity of the environmental changes were not great enough to affect the successional stage. Consistency in the successional stages 1 or 2 were involved, never with successional stage 3 or with successional stage 4, which was only observed once. This appears to indicate that only the initial successional stages are sometimes impervious to environmental changes.

Possible environmental modifications which are biologically induced include: current modification due to the baffling effects of crinoid stands, modification of the substrate due to the activities of deposit feeding organisms, and the paving of an initially soft substrate by the hard skeletal material derived from organisms of a preceding successional stage.

From the above discussion several conclusions may be drawn. First, both autogenic and allogenic succession appear to take place within the Lodgepole. Second, the transition from a barren surface to stage 1, and the transition from stage 1 to stage 3 appear to be the result of autogenic causes, since these transitions only occur when there is no change in rock type. The autogenic cause for the transition from a barren surfaces to a pioneering stage have been

documented by Walker and Alberstadt (1975) and Bretsky and Bretsky (1975). Third, the transition from successional stage 2 to successional stage 3 and the transition from stage 1 to stage 4, appear to be the result of allogenic causes, since, these transitions only occur where there is a change in the rock type. These two transitions agree with a conclusion by Johnson (1972), in which he observed that physical perturbations do not always downgrade succession, but may permit the attainment of a new stage not previously attained. Fourth, the transition from a barren surface to stage 2 and the transition from stage 1 to stage 2 appear to result from either autogenic or allogenic changes. Finally, early successional stages appear to be less susceptible to changes in the physical environment than later successional stages.

The successional sequence described previously is not an invariant, unidirectional sequence. As can be seen in Appendix 1, downgrading to a previous stage of succession or to a barren bedding surface, occurred twenty-four times. Johnson (1972, p. 152) stated "Any disturbance that affects the species composition will downgrade the community to an earlier stage of succession." As with succession in a "forward" direction, the disturbances which cause retrogression can also be placed into two categories: biologically induced, by the activities of the organisms within the community (autogenic); and physical disturbances (allogenic).

In order to determine to what extent autogenic and allogenic disturbances cause downgrading, the same approach used above to evaluate the concepts of allogenic and autogenic succession, will be

used. Downgrading to a lower successional stage with an accompanying change in rock type occurred six times, and is considered to represent a retrogression due to allogenic causes. As previously described the various rock types within the study section are probably the result of different energy regimes. Therefore, the regression appears to be the result of changing energy conditions. Hurd and Wolf (1974) in studies involving modern plant communities, found that the higher the diversity in a community, the less resilient it is to sudden perturbations. Observed downgrading due to physical causes includes downgrading: from stage 2 to a barren substrate; from stage 2 to stage 1; and from stage 3 to stage 1.

Downgrading to a previous successional stage without a change in the rock type occurred eighteen times within the study section, and is thought to represent regression due to autogenic causes. Odum (1975, p. 162) stated that observations in climax forest communities suggests that self-destructive biological changes, which in an individual would be termed aging, may be taking place. Examples of such self-destructive changes are that young organisms may not be replacing the older organisms as they die, and that the recycling of essential nutrients may have slowed to a potentially destructive rate in climax communities. Another factor which may relate to the stability of the various successional stage is their trophic structure. As will be shown in a following section, as succession proceeds from stage 1 to stage 3, the proportion of the population composed of filter-feeders increased relative to the proportion of the population composed of deposit-feeders. According to Levinton (1972), suspension

feeding communities are characterized by poor stability, whereas in communities dominated by deposit feeders, stability is relatively high. Bretsky (1969, p. 45) suggested that invertebrate communities which are adapted to monotonous off-shore environments tend to be composed of stenotypic taxa, and that slight changes in physical or biotic selective pressures could disrupt the community. Observed downgrading due to autogenic causes include downgrading from stage 3 to stage 2; from stage 2 to stage 1; from stage 2 to a barren surface; and from stage 1 to a barren surface.

From the above discussion it appears that retrogression to previous successional stages is the result of both allogenic and autogenic causes. Downgrading which appears to be due to autogenic causes includes downgrading: from stage 3 to stage 2; and from stage 1 to a barren surface. Downgrading which appears to be due to allogenic causes includes the downgrading from stage 3 to stage 1. Downgrading from stage 2 to stage 1 and from stage 2 to a barren surface, appears to have resulted from either autogenic or allogenic causes.

Conclusions reached within this section should be viewed with caution, especially transitions between successional stages which skip intermediate stages. This is because, what was observed in the field was faunal changes from bedding surface to bedding surface, and succession or retrogression may have proceeded rapidly enough so that the intermediate stages may have taken place, but are contained within the beds and not seen at the bedding surface.

Trends in Diversity and Calcified Biovolume

With Succession

Odum (1971) and Walker and Alberstadt (1975) have suggested that certain biological parameters of a community vary in a predictable manner during the course of succession. These parameters and the ways in which they vary are shown in Figs. 1 and 2. For the present study, two of these trends, diversity and biovolume, may be examined.

According to both Odum (1971) and Walker and Alberstadt (1975), species diversity increases during the early stages of succession, and then stabilizes or declines in the later stages. To test this predicted trend, diversity was calculated in two ways, first in terms of richness and secondly in terms of dominance diversity. The trend shown by each of these two types of diversity with succession will be discussed separately, starting with richness (Plate 2).

As succession proceeds from stage 1 through stage 3, the mean values for the richness of each of the stages is as follows: Stage 1, 3.5; stage 2, 4.21; and stage 3, 4.67. However, a one-way analysis of variance using an F-test at a 95% confidence level suggests that this increasing trend in richness may not exist, as the mean values are not statistically different from one another. Therefore, these results suggest that richness may remain constant with succession, which is in disagreement with the predicted trends of Odum (1971) and Walker and Alberstadt (1975).

For dominance-diversity the mean values for each of the first

three successional stages are as follows: stage 1, 0.53; stage 2, 0.92; and stage 3, 1.19. A one-way analysis of variance using an F-test at a 95% confidence level indicates that the mean values for dominance-diversity of stage 1 and stage 2 and of stage 1 and stage 3 are statistically different, and that there is no statistically significant difference between the mean values of stage 2 and stage 3. The trend in dominance diversity suggested by this study is one of an increase from early stages of succession and a stabilization in later stages of succession, and therefore agrees with the predicted trends of Odum (1971) and of Walker and Alberstadt (1975).

For biomass, Odum (1971) predicted an increasing trend as a community undergoes succession from a pioneering stage to a climax stage. For the purpose of this study, biomass was measured in terms of the volume of calcified skeletal material present on the studied bedding surfaces. Results of this analysis showed that the range and mean values for the calcified biovolume of each of the three successional stage varied as follows: stage 1, 3.7 milliliters to 37.5 milliliters, 13 milliliters; stage 2, 5.8 milliliters to 445.7 milliliters, 276 milliliters, and stage 3, 2523.6 milliliters to 9107.8 milliliters, 4194 milliliters. At a 95% confidence level, a one-way analysis of variance using an F-test suggests that the mean values for each of the three successional stages are statistically different from one another. Therefore, observations made in this study appear to support the prediction of increasing biomass with succession.

Changes in the Trophic Structure with Succession

As succession proceeds, variations in the trophic structure between each of the four stages can be seen (Fig. 37). In successional stage 1, epifaunal suspension feeders are the dominant trophic group in terms of the number of species belonging to each trophic group. Following this group, in decreasing abundance, are the epifaunal deposit feeders and the infaunal deposit feeders. Successional stage 2 includes the loss of the infaunal deposit feeders and the addition of two new trophic groups, the infaunal suspension feeders, and the nektic carnivores. In terms of the percent of the population belonging to each trophic group, the epifaunal suspension feeders are still the dominant trophic group, increasing slightly from stage 1. This group is then followed, in decreasing abundance, by epifaunal deposit feeders, infaunal suspension feeders and nektic carnivores. In stage 3, nektic carnivores and infaunal suspension feeders are not preserved, leaving only two trophic groups, the epifaunal suspension feeders, which increased in importance from stage 2, and the epifaunal deposit feeders. Successional stage 4 is represented by three groups, the epifaunal suspension feeders which are the dominant group, the infaunal deposit feeders, and the nektic carnivores. Thus, from stage 1 to stage 3, the overall trend appears to be one of an increase in the proportion of the community which are suspension feeders relative to the proportion of the community which are deposit feeders.

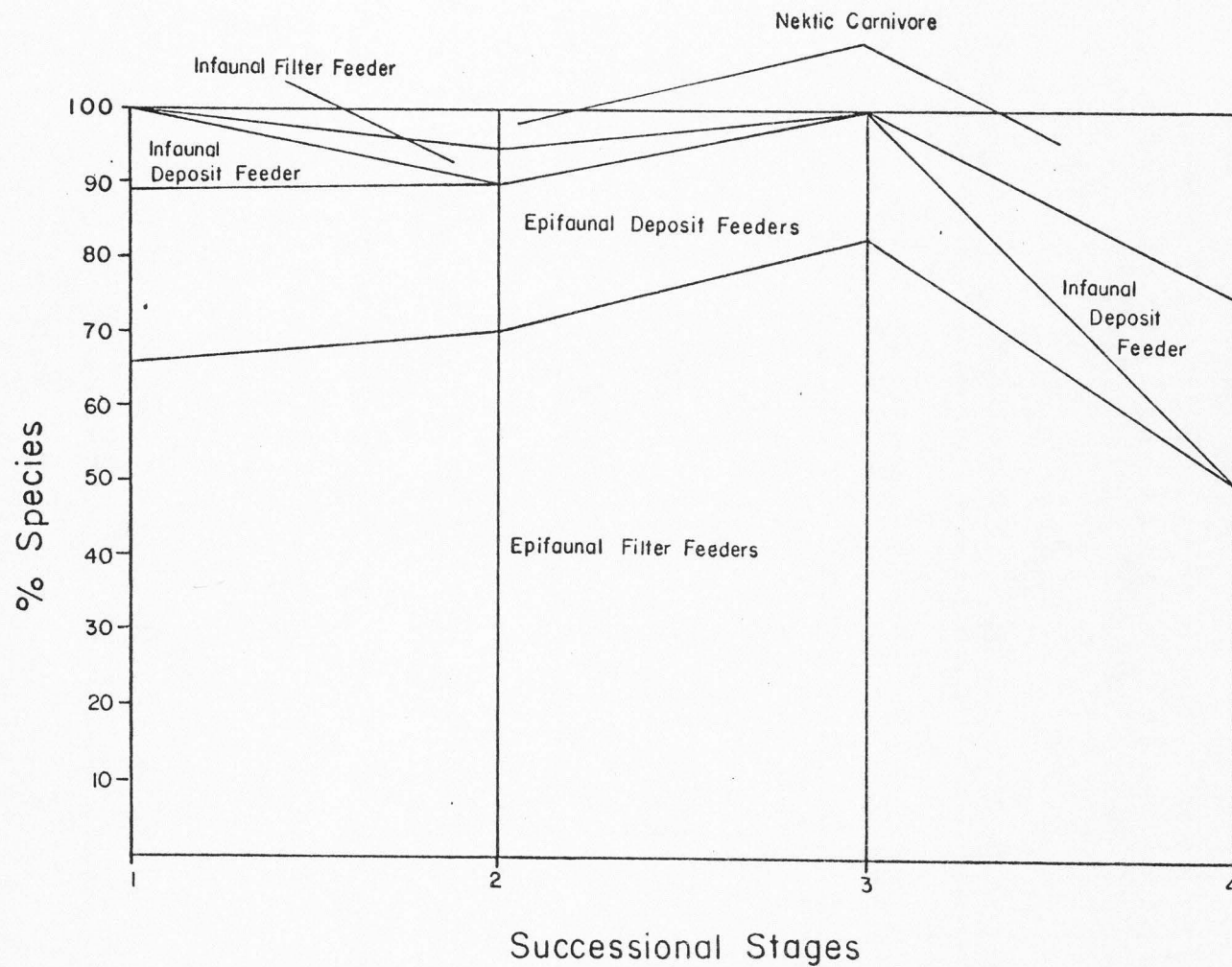


Figure 37. Changes in the trophic structure with succession.

SUMMARY

Physical and biological evidence suggest that this Early Mississippian sequence of carbonate rocks was deposited in relatively deep water, below effective wave base, but above the zone of oxygen depletion, and under the influence of a weak unidirectional current or multi-directional currents of similar competency. The substrate is thought to have been composed of carbonate mud, with the $Eh=0$ line being located just below the sediment-water interface for most of Lodgepole time. Evidence also suggests a very low sedimentation rate.

Variations in these general conditions are indicated by the different rock types present within the study section, with packstones indicating higher energy conditions, mudstones indicating lower energy conditions, and wackestones indicating energy conditions intermediate between those of the packstones and mudstones.

Three faunal associations, along with several sub-associations are indicated by the clustering of indices of affinity. These associations include: (1) Zaphrentis-Crinoid-Syringopora-Euomphalus-Echinoid-Cleiothyridina-Unispirifer-Orthotetes-Lithostrotionella-Flexaria-Camarotoechia-Schizophoria; (2) Cruziana-Dwelling tube; (3) Shark-Blastoid-Helminthopsis.

Based on the examination of bedding surfaces directly following barren bedding surfaces, four successional stages are recognized.

Because changes in the faunal composition between the various successional stages appear to take place both with, and without lithologic change, it is concluded that succession may result from either biological modification of the environment, or from physical changes. Therefore, succession was both autogenically or allo-genically controlled.

As succession proceeded through the successional sequence, the values for diversity and calcified biovolume increased. This trend is in agreement with the previously predicted trends of Walker and Alberstadt (1975).

The overall trend observed in the trophic structure with faunal succession appears to be one of an increase in the proportion of the community which are suspension feeders relative to the proportion of the community which are deposit feeders.

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APPENDIX

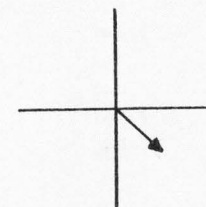
Appendix Results of faunal analysis: Orientation/Preservation

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams ¹	Resulting Vector Direction and Magnitude
125	C	0	-	-
124	C	0	-	-
123	C	0	-	-
122	C	0	-	-
121	C	0	-	-
120	-	0	-	-
119	C	0	-	-
118	C	0	-	-
117	C	0	-	-

116



C

4



¹ North towards top of diagrams

Appendix Con't


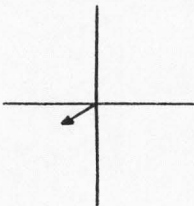
Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
115	C	0	-	-
114	C	0	-	-
113	C	0	-	-
112	C	0	-	-
111	C	0	-	-
110	B	0	-	-
109	C	0	-	-
108	C	5		
107	B	0	-	-
106	A	0	-	-

Appendix

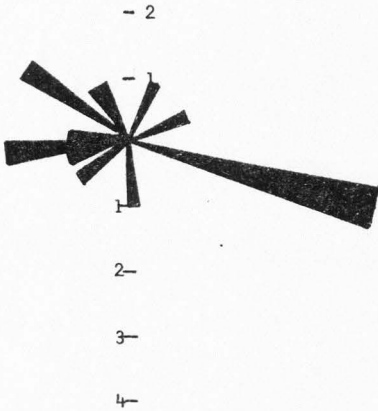
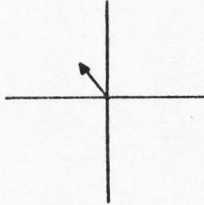
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Bed	Crinoid Deposit	Number of Orientation Measurements	<u>Orientational Data</u>	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
105	B	0	-	-
104	B	0	-	-
103	C	0	-	-
102	C	0	-	-
101	B	0	-	-
100	B	0	-	-
99	C	0	-	-
98	B	0	-	-
97	-	0	-	-
96	C	0	-	-
95	B	0	-	-
94	B	0	-	-
93	C	0	-	-
92	B	0	-	-


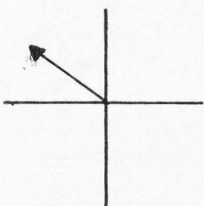
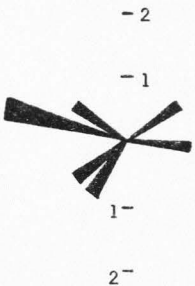
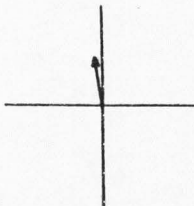
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Bed	Crinoid Deposit	Number of Orientation Measurements	<u>Orientational Data</u>	
			Resulting Rose Diagram	Resulting Vector Direction and Magnitude
91	B	0	-	-
90	B	0	-	-
89	B	0	-	-
88	B	0	-	-
87	C	8		
86	B	0	-	-
85	C	0	-	-
84	C	0	-	-
83	D	0	-	-


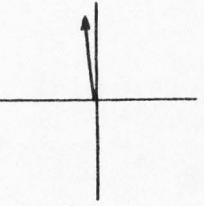

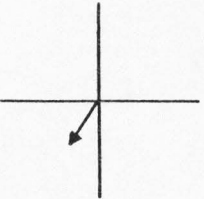


Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
82	C	16		
81	B	0	-	-
80	C	0	-	-
79	C	0	-	-
78	B	0	-	-
77	A	0	-	-
76	C	0	-	-


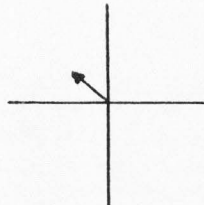

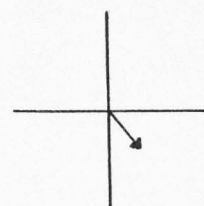
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			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
75	C	0	-	-
74	D	0	-	-
73	C	12		
72	C	0	-	-
71	C	7		

Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
70	C	6		
69	D	0	-	-
68	C	5		
67	C	4		

Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
66	C	0	-	-
65	B	0	-	-
64	C	0	-	-
63	C	6		
62	C	0	-	-
61	C	7		
60	C	0	-	-

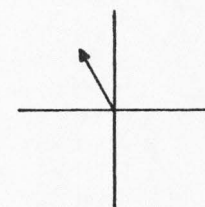
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Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude

59

B

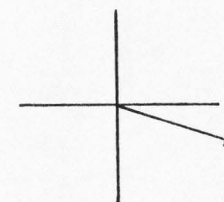
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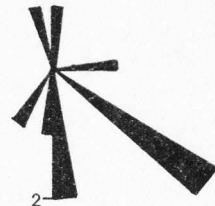
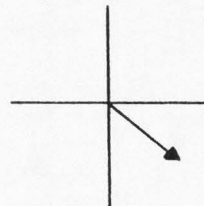

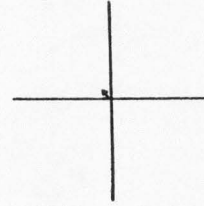
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C

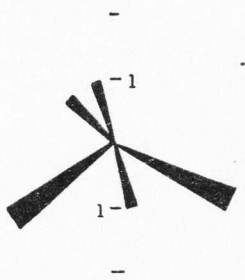
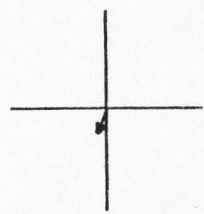
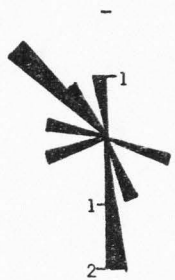
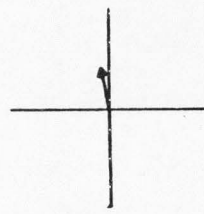
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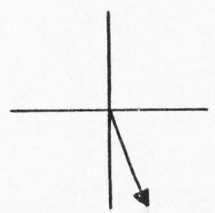

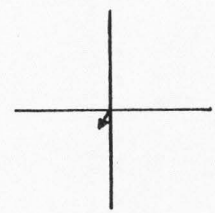
Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
57	B	0	-	-
			-	
			-	
56	C	10		
			3-	
			-2	
55	C	6		
			1-	
			2-	


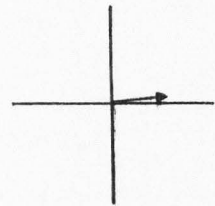

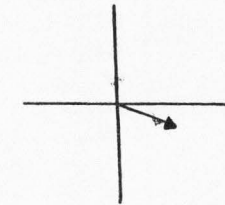

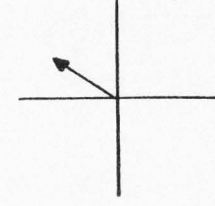
Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	<u>Orientational Data</u>	
			Resulting Rose Diagrams	Resulting vector Direction and Magnitude
54	C	7		
53	C	10		
52	B	0	-	-
51	C	0	-	-


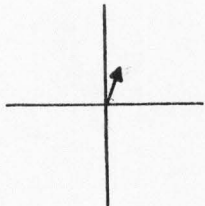
Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
50	B	10		
49	C	3		
48	C	0	-	-
47	C	0	-	-


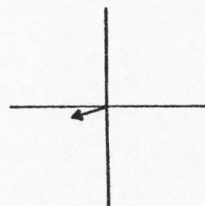

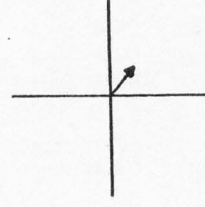

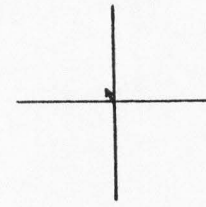
Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
46	C	3		
45	C	6		
44	C	6		
43	B	0	-	-
42	B	0	-	-
41	C	0	-	-


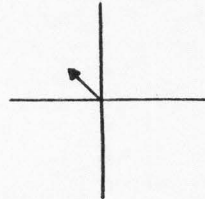

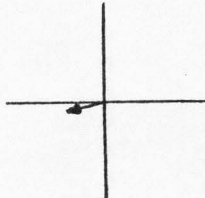
Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	<u>Orientational Data</u>	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
40	B	0	-	-
39	C	0	-	-
38	C	0	-	-
37	C	0	-	-
36	-	0	-	-
35	B	0	-	-
34	-	0	-	-
33	C	0	-	-
32	C	0	-	-
31	-	0	-	-
30	C	5		

Appendix Con't


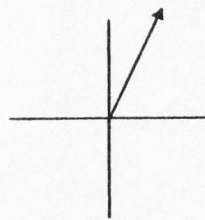
Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
29	-	0	-	-
28	C	0	-	-
27	-	4		
26	-	10		
25	B	5		

Appendix 1. Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	Orientational Data	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
24	B	0	-	-
23	C	0	-	-
22	B	0	-	-
21	C	0	-	-
20	B	0	-	-
19	B	5		
18	C	6		

Appendix Con't				
Bed	Crinoid Deposit	Number of Orientation Measurements	<u>Orientational Data</u>	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
17	-	0	-	-
16	B	0	-	-
15	-	0	-	-
14	-	0	-	-
13	B	0	-	-
12	C	0	-	-
11	-	0	-	-
10	B	0	-	-
9	B	0	-	-
8	B	0	-	-

Appendix Con't

Bed	Crinoid Deposit	Number of Orientation Measurements	<u>Orientational Data</u>	
			Resulting Rose Diagrams	Resulting Vector Direction and Magnitude
7	C	14		
6	C	0	-	-
5	-	0	-	-
4	B	0	-	-
3	D	0	-	-
2	C	0	-	-
1	D	0	-	-

Bed	Thickness (cm)	Description ¹	Successional	Σ Insolubles	Σ Organics
			Stage ²		
125		Packstone, dark gray (N3), vcmx, structureless, contains dark gray (N3) siliceous nodules	4		
124	38.1	Wackestone, medium gray (N5), mxn to cxn, structureless	1		
123	27.9	Wackestone, medium light gray (N6), mxn to cxn, structureless	2		
122	76.2	Packstone, medium light gray (N6), mxn to cxn, structureless	1		
121	40.6	Packstone, light gray (N7), cxn, structureless	1		
120	25.4	Wackestone, medium dark gray (N4), fxn to mxn, structureless	1		
119	61.0	Wackestone, medium light gray (N6), mxn to cxn, structureless	2		
118	40.6	Wackestone, medium light gray (N6), fxn, structureless, contains dark gray (N3) siliceous nodules	2		
117	30.5	Mudstone, medium gray (N5), fxn, structureless, contains dark gray (N3) siliceous nodules	1		
116	91.4	Crystalline limestone, light gray (N7), cxn, structureless	2		
115	35.6	Mudstone, medium dark gray (N4), vfxn, structureless, contains dark gray (N3) siliceous nodules	2		
114	10.2	Mudstone, medium dark gray (N4), vfxn, structureless, contains dark gray (N3) siliceous nodules	1		
113	30.5	Wackestone, medium dark gray (N4), vfxn, structureless	3		
112	15.2	Mudstone, medium dark gray (N4), vfxn, structureless, contains dark gray (N3) siliceous nodules	2		
111	10.2	Mudstone, medium dark gray (N4), vfxn, structureless	2		
110	30.5	Wackestone, dark gray (N3), vfxn, structureless, contains dark gray (N3) siliceous nodules	2		
109	40.6	Mudstone, medium dark gray (N4), vfxn, structureless, contains dark gray (N3) siliceous nodules	2		
108	30.5	Wackestone, dark gray (N3), vfxn, structureless, contains dark gray (N3) siliceous nodules	2		
107	27.9	Mudstone, dark gray (N3), vfxn, structureless	2		
106	25.4	Mudstone, medium dark gray (N4), vfxn, structureless	2		
105	12.7	Mudstone, medium dark gray (N4), vfxn, structureless	2		
104	30.5	Mudstone, medium dark gray (N4), fxn, structureless, contains dark gray (N3) siliceous nodules	2		
103	12.7	Mudstone, medium dark gray (N4), fxn, structureless	2		
102	15.2	Wackestone, medium gray (N5), fxn, structureless	2		
101	48.3	Wackestone, medium gray (N5), fxn, structureless	2		
100	38.1	Wackestone, medium dark gray (N4), vfxn, laminated (.2 cm), to structureless at the top	2		
99	17.8	Wackestone, medium dark gray (N4), vfxn, structureless	2		
98	15.2	Wackestone, medium dark gray (N4), cxn, structureless	2		
97	43.2	Wackestone, medium light gray (N6), fxn, laminated (.2-.5 cm)	2		
96	15.2	Wackestone, medium gray (N5), fxn to mxn, structureless	2		
95	10.2	Wackestone, medium gray (N5), fxn, laminated (.1-.3 cm)	1		
94	30.5	Wackestone, medium gray (N5), fxn, laminated (.2-.3 cm)	2		
93	66.0	Wackestone, medium gray (N5), fxn to mxn, structureless	2		
92	34.3	Wackestone, medium gray (N5), vfxn to fxn, structureless	2		
91	15.2	Wackestone, medium gray (N5), mxn to cxn, laminated (.1-.3 cm)	2		
90	11.4	Wackestone, medium dark gray (N4), mxn, laminated (.1 cm)	2		
89	10.2	Wackestone, medium dark gray (N4), fxn, structureless	3		
88	22.9	Wackestone, medium dark gray (N4), fxn to mxn, laminated (.1-.3 cm)	2		
87	12.7	Wackestone, medium dark gray (N4), vfxn, structureless	2		
86	15.2	Packstone, medium dark gray (N4), cxn, structureless	2		
85	15.2	Wackestone, medium dark gray (N4), vfxn, structureless	2		
84	25.4	Mudstone, medium gray (N5), vfxn, structureless	2		
83	15.2	Wackestone, medium gray (N5), vfxn, laminated (.3 cm)	1		
82	30.5	Wackestone, medium dark gray (N4), fxn to mxn, structureless	2		
81	45.7	Wackestone, medium dark gray (N4), fxn, structureless	3		
80	12.7	Wackestone, medium gray (N5), fxn, structureless	2		
79	12.7	Wackestone, medium gray (N5), mxn, structureless	2		
78	33.0	Wackestone, medium dark gray (N4), vfxn to fxn, laminated (.2-.3 cm)	2		
77	17.8	Wackestone, medium dark gray (N4), fxn, structureless	-		
76	30.5	Packstone, medium dark gray (N4), mxn, laminated (.15-.6 cm)	2		
75	17.8	Packstone, medium dark gray (N4), mxn, laminated (.1 cm)	2		
74	12.7	Wackestone, medium gray (N5), fxn, laminated (.3 cm)	-		
73	20.3	Wackestone, medium dark gray (N4), mxn, laminated (.1 cm)	2		
72	38.1	Mudstone, medium gray (N5), fxn, laminated (.1 cm)	2		
71	53.5	Wackestone, medium gray (N5), mxn, laminated (.1 cm), with cross-bedding	2		
70	33.0	Wackestone, medium gray (N5), mxn to cxn, laminated (.1-.2 cm)	2		
69	34.3	Mudstone, medium gray (N5), fxn, laminated (.1 cm)	-		
68	38.1	Wackestone, medium gray (N5), mxn, structureless	2		
67	15.2	Wackestone, medium dark gray (N4), mxn, structureless	2		
66	12.7	Mudstone, dark gray (N3), vfxn to fxn, structureless	2		
65	17.8	Wackestone, medium dark gray (N4), fxn, laminated (.1-.3 cm)	2		
64	40.6	Wackestone, medium dark gray (N4), fxn, laminated (.5 cm)	2		
63	40.6	Wackestone, medium gray (N5), cxn, structureless	2		
62	12.7	Wackestone, medium dark gray (N4), fxn, structureless	2		
61	22.9	Wackestone, medium dark gray (N4), fxn to mxn, structureless	2		
60	19.1	Wackestone, medium gray (N5), cxn, laminated (.2 cm)	2		
59	35.6	Wackestone, medium dark gray (N4), mxn to cxn, laminated (.2 cm)	2		
58	30.5	Wackestone, medium gray (N5), mxn to cxn, laminated (.2 cm)	2		
57	8.9	Wackestone, dark gray (N3), fxn to mxn, laminated (.1 cm)	1		
56	7.6	Wackestone, medium dark gray (N4), fxn to mxn, structureless	2		
55	22.9	Wackestone, medium dark gray (N4), fxn, laminated (.1 cm)	3		
54	22.9	Wackestone, dark gray (N3) to medium dark gray (N4), fxn, laminated (.1-.2 cm)	3		
53	12.7	Wackestone, medium dark gray (N4), fxn, laminated (.1-.2 cm)	2		
52	43.2	Wackestone, medium dark gray (N4), fxn, laminated (.1-.2 cm)	3		
51	27.9	Wackestone, medium dark gray (N4), fxn, laminated (.2 cm)	2		
50	12.7	Wackestone, medium dark gray (N4), fxn to mxn, laminated (1.5-2.0 cm)	2		
49	17.8	Wackestone, medium dark gray (N4), fxn, laminated (.3 cm)	2		
48	7.6	Wackestone, medium dark gray (N4), fxn, structureless	2		
47	30.5	Wackestone, medium dark gray (N4), fxn, laminated (.3 cm)	2		
46	22.9	Wackestone, medium gray (N5), fxn, laminated (.2 cm)	2		
45	15.2	Wackestone, medium dark gray (N4), fxn, structureless	2		
44	22.9	Wackestone, medium gray (N5), fxn to mxn, laminated (.1-.2 cm)	3		
43	22.9	Wackestone, medium light gray (N6), fxn to mxn, laminated (.1 cm)	2		
42	35.6	Wackestone, medium gray (N5), fxn, laminated (.1-.3 cm)	1		
41	30.5	Wackestone, medium dark gray (N4), fxn, laminated (.1 cm)	2		
40	20.3	Wackestone, medium gray (N5), fxn, laminated (.2 cm)	1		
39	30.5	Wackestone, medium gray (N5), fxn, laminated (.4 cm)	1		
38	12.7	Wackestone, medium gray (N5), cxn, structureless	2		
37	15.2	Wackestone, medium dark gray (N4), fxn to mxn, structureless	2		
36	15.2	Mudstone, medium gray (N5), fxn, structureless	-		
35	16.5	Wackestone, medium dark gray (N4), fxn to mxn, structureless	2		
34	17.8	Wackestone, medium dark gray (N4), fxn, structureless	2		
33	55.9	Mudstone, medium dark gray (N4), fxn, laminated (.3-.5 cm)	2		
32	30.5	Wackestone, medium dark gray (N4), fxn, laminated (.1-.2 cm), contains dark gray (N3) siliceous nodules	2		
31	55.9	Mudstone, medium gray (N5), fxn, laminated (.1 cm), contains dark gray (N3) siliceous nodules	2		
30	20.3	Wackestone, medium gray (N5), mxn to cxn, structureless, contains dark gray (N3) siliceous nodules	2		
29	33.0	Mudstone, medium gray (N5), fxn, laminated (.1 cm)	-		
28	22.9	Wackestone, medium dark gray (N4), fxn, laminated (.1 cm)	2		
27	19.1	Wackestone, medium gray (N5), mxn, structureless	2		
26	25.4	Wackestone, medium gray (N5), mxn, laminated (.3 cm)	2		
25	55.9	Packstone, medium gray (N5), cxn, laminated (.2 cm)	2		
24	19.5	Wackestone, medium gray (N5), fxn, laminated (.3-.5 cm)	1		
23	20.3	Wackestone, medium gray (N5), fxn to mxn, laminated (.1 cm)	1		
22	25.4	Wackestone, medium gray (N5), fxn, laminated (.1-.2 cm)	2		
21	38.1	Wackestone, medium dark gray (N4), fxn, laminated (.1-.3 cm)	2		
20	8.9	Wackestone, medium dark gray (N4), fxn to mxn, structureless, contains dark gray (N3) siliceous nodules	2		
19	45.7	Wackestone, medium gray (N5), fxn to mxn, laminated (.2 cm)	2		
18	49.5	Wackestone, medium dark gray (N4), fxn to mxn, laminated (.1 cm)	2		
17	11.4	Wackestone, medium gray (N5), fxn, laminated (.2 cm)	-		
16	5.1	Wackestone, medium gray (N5), fxn, laminated (.2 cm)	1		
15	11.4	Wackestone, medium gray (N5), fxn, structureless	-		
14	5.1	Wackestone, medium dark gray (N4), laminated (.2 cm)	-		
13	10.1	Wackestone, medium dark gray (N4), fxn, laminated (.1 cm)	1		
12	6.4	Wackestone, medium dark gray (N4), fxn, laminated (.1 cm)	1		
11	6.4	Wackestone, medium dark gray (N4), fxn, structureless	-		
10	6.4	Wackestone, medium dark gray (N4), laminated (.1 cm)	1		
9	21.6	Wackestone, medium dark gray (N4), mxn, laminated (.1 cm)	1		
8	8.9	Wackestone, medium dark gray (N4), fxn, structureless	1		
7	20.3	Packstone, medium gray (N5), mxn, laminated (.2 cm)	2		
6	12.7	Wackestone, medium gray (N5), fxn, laminated (.1 cm)	2		
5	6.4	Wackestone, medium gray (N5), fxn, laminated (.1 cm)	2		
4	7.6	Wackestone, medium dark gray (N4), fxn, structureless	1		
3	17.8	Wackestone, medium dark gray (N4), fxn, laminated (.1 cm)	-		
2	15.2	Wackestone, medium gray (N5), fxn, laminated (.2 cm)	2		
1	25.4	Wackestone, medium gray (N5), fxn, structureless	-		

1 All beds are fossiliferous unless noted

2 For explanation see page

Bed	Taxa	Trophic Niche ¹	Successional Stage ²	Surface Area (m ²)	DT	Diversity	DE	Log of Total Calcified Biovolume
125	Crinoids Elastoids Shark Helminthopsis	VHF VHF NC MED	4	0.22				
124	Crinoid	VHF	1	0.22				
123	Zaphrentis Crinoid Spirifer	IF VHF IF	2	0.63				
122	Crinoid Unispirifer Spirifer	VHF IF IF	1	0.49				
121	Crinoid Spirifer	VHF IF	1	0.36				
120	Spirifer	IF	1	0.14				
119	Zaphrentis Crinoid	IF VHF	2	0.52				
118	Zaphrentis Crinoid Unispirifer Flexaria Spirifer	IF VHF IF VLF IF	2	0.53				
117	Zaphrentis Crinoid	IF VHF	2	0.18				
116	Zaphrentis Crinoid Unispirifer Composita	IF VHF IF IF	2	1.32				
115	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.22				
114	Crinoid Schizophoria	VHF IF	1	0.13				
113	Lithostrotionella Zaphrentis Syringopora Crinoid Euomphalus Camarotoechia Flexaria Spirifer Schizophoria	HF IF HF VHF MED LF VLF IF IF	3	1.24				
112	Zaphrentis Crinoid Shark Unispirifer Camarotoechia Schizophoria	IF VHF NC IF LF IF	2	1.40				
111	Syringopora Crinoid	HF VHF	2	0.74				
110	Zaphrentis Syringopora Crinoid Unispirifer	IF HF VHF IF	2	0.60				
109	Zaphrentis Crinoid Unispirifer Schizophoria	IF VHF IF IF	2	0.79				
108	Zaphrentis Syringopora Crinoid Spirifer Schizophoria	IF HF VHF IF IF	2	0.55				
107	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.12				
106	Zaphrentis Syringopora Crinoid Schizophoria	IF HF VHF IF	2	0.87				
105	Zaphrentis Crinoid	IF VHF	2	0.12				
104	Zaphrentis Syringopora Crinoid Unispirifer Camarotoechia Spirifer	IF HF VHF IF LF IF	2	0.87				
103	Syringopora Crinoid	HF VHF	2	0.15				
102	Zaphrentis Syringopora Crinoid Euomphalus Unispirifer	IF HF VHF MED IF	2	0.77				
101	Zaphrentis Crinoid Orthotetes	IF VHF IF-VLF	2	0.72				
100	Zaphrentis Syringopora Crinoid Spirifer	IF HF VHF IF	2	0.33				
99	Zaphrentis Syringopora Crinoid Schizophoria	IF HF VHF IF	2	0.29				
98	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.17				
97	Zaphrentis Euomphalus Cruziana	IF HF MED MED	2	0.48				
96	Zaphrentis Crinoid	IF VHF	2	0.05				
95	Crinoid Spirifer Helminthopsis	VHF IF MED	1	0.17				
94	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.71				
93	Zaphrentis Crinoid Flexaria Orthotetes	IF VHF VLF IF-VLF	2	0.18				
92	Zaphrentis Syringopora Crinoid Euomphalus Spirifer	IF HF VHF MED IF	2	0.28				
91	Zaphrentis Syringopora Crinoid Spirifer	IF HF VHF IF	2	0.36				
90	Zaphrentis Crinoid Orthotetes Spirifer	IF VHF IF-VLF IF	2	0.12				
89	Lithostrotionella Zaphrentis Syringopora Crinoid Euomphalus Orthotetes Spirifer	HF IF HF VHF MED IF-VLF IF	3	0.40				
88	Zaphrentis Syringopora Crinoid Unispirifer Spirifer	IF HF VHF IF IF	2	0.21				
87	Zaphrentis Syringopora Crinoid Unispirifer	IF HF VHF IF	2	0.29				
86	Zaphrentis Crinoid Spirifer Orthotetes	IF VHF IF IF-VLF	2	0.46				
85	Zaphrentis Syringopora Crinoid Spirifer Zoophycus	IF HF VHF IF IF	2	0.26				
84	Zaphrentis Crinoid Spirifer Schizophoria	IF VHF IF IF	2	0.17				
83	Cruziana	MED	1	0.07				
82	Zaphrentis Crinoid Unispirifer	IF VHF IF	2	0.32				
81	Lithostrotionella Zaphrentis Syringopora Crinoid Orthotetes	HF IF HF VHF IF-VLF	3	0.12				
80	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.43				
79	Zaphrentis Syringopora Crinoid Orthotetes	IF HF VHF IF-VLF	2	0.14				
78	Zaphrentis Crinoid	IF VHF	2	0.04				
77	-	-	-	0.03				
76	Zaphrentis Syringopora Crinoid Orthotetes Spirifer	IF HF VHF IF-VLF IF	2	0.36				
75	Syringopora Crinoid	HF VHF	2	0.15				
74	-	-	-	0.20				
73	Zaphrentis Syringopora Crinoid Orthotetes	IF HF VHF IF-VLF	2	0.72				
72	Zaphrentis Crinoid Orthotetes	IF VHF IF-VLF	2	0.30				
71	Zaphrentis Syringopora Crinoid Unispirifer	IF HF VHF IF	2	0.24				
70	Zaphrentis Syringopora Crinoid Orthotetes Unispirifer	IF HF VHF IF-VLF IF	2	0.23				
69	-	-	-	0.08				
68	Zaphrentis Syringopora Crinoid Flexaria	IF HF VHF VLF	2	0.20				
67	Zaphrentis Syringopora Crinoid Euomphalus Orthotetes Cleiothyridina Unispirifer	IF HF VHF MED IF-VLF LF IF	2	0.30				
66	Zaphrentis Syringopora Crinoid Orthotetes	IF HF VHF IF-VLF	2	0.16				
65	Syringopora Crinoid	HF VHF	2	0.30				
64	Zaphrentis Syringopora Crinoid Composita Spirifer	IF HF VHF LF IF	2	0.25				
63	Zaphrentis Crinoid	IF VHF	2	0.40				
62	Zaphrentis Crinoid Euomphalus Echinoid Flexaria	IF VHF MED MED VLF	2	0.29				
61	Zaphrentis Syringopora Crinoid Spirifer	IF HF VHF IF	2	0.32				
60	Zaphrentis Syringopora Crinoid Echinoid Orthotetes Unispirifer	IF HF VHF MED IF-VLF IF	2	0.35				
59	Zaphrentis Crinoid Echinoid	IF VHF MED	2	0.29				
58	Zaphrentis Crinoid Euomphalus	IF VHF MED	2	0.29				
57	Crinoid	VHF	1	0.09				
56	Zaphrentis Syringopora Crinoid Euomphalus Orthotetes	IF HF VHF MED IF-VLF	2	0.15				
55	Lithostrotionella Zaphrentis Syringopora Crinoid Echinoid Orthotetes	HF IF HF VHF MED IF-VLF	3	0.75				
54	Lithostrotionella Zaphrentis Syringopora Crinoid Echinoid Orthotetes	HF IF HF VHF MED IF-VLF	3	0.19				
53	Zaphrentis Syringopora Crinoid Echinoid	IF HF VHF MED	2	0.53				
52	Lithostrotionella Zaphrentis Crinoid	HF IF VHF	3	0.24				
51	Zaphrentis Syringopora Crinoid Euomphalus Unispirifer	IF HF VHF MED IF	2	0.51				
50	Zaphrentis Syringopora Crinoid Euomphalus Orthotetes	IF HF VHF MED IF-VLF	2	0.22				
49	Zaphrentis Crinoid Euomphalus	IF VHF MED	2	0.15				
48	Syringopora Crinoid Orthotetes Spirifer	HF VHF IF-VLF IF	2	0.15				
47	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.18				
46	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.10				
45	Zaphrentis Syringopora Crinoid Euomphalus	IF HF VHF MED	2	0.16				
44	Lithostrotionella Zaphrentis Syringopora Crinoid Flexaria Spirifer	HF IF HF VHF VLF IF	3	0.13				
43	Zaphrentis Syringopora Crinoid Euomphalus Echinoid Cleiothyridina Unispirifer	IF HF VHF MED MED LF	2	0.13				
42	Crinoid Unispirifer Helminthopsis	VHF IF MED	1	0.30				
41	Zaphrentis Syringopora Crinoid Euomphalus Unispirifer Spirifer Cruziana Dwelling Tube	IF HF VHF MED IF LF VLF SP?	2	0.28				
40	Crinoid Unispirifer	VHF IF	1	0.20				
39	Crinoid Echinoid	VHF MED	1	0.52				
38	Zaphrentis Syringopora Crinoid Unispirifer	IF HF VHF IF	2	0.15				
37	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.18				
36	-	-	-	0.11				
35	Zaphrentis Syringopora Crinoid Unispirifer	IF HF VHF IF	2	0.19				
34	Zaphrentis Syringopora	IF HF	2	0.31				
33	Syringopora Crinoid Euomphalus Cleiothyridina Unispirifer	HF VHF VHF LF IF	2	0.52				
32	Syringopora Crinoid Unispirifer	HF VHF IF	2	0.59				
31	Zaphrentis Syringopora Euomphalus	IF HF MED	2	0.47				
30	Zaphrentis Syringopora Crinoid Cleiothyridina	IF HF VHF LF	2	0.50				
29	-	-	-	0.30				
28	Syringopora Crinoid Cleiothyridina	HF VHF VLF	2	0.30				
27	Zaphrentis Syringopora Euomphalus Cleiothyridina Unispirifer Camarotoechia	IF HF MED LF IF LF	2	0.23				
26	Zaphrentis Syringopora Euomphalus Cleiothyridina	IF HF MED LF	2	0.22				
25	Zaphrentis Syringopora Crinoid	IF HF VHF	2	0.28				
24	Crinoid Unispirifer	VHF IF	1	0.03				
23	Crinoid Orthotetes Unispirifer	VHF IF-VLF IF	1	0.03				
22	Syringopora Crinoid Euomphalus	HF VHF MED	2	0.15				
21	Syringopora Crinoid Euomphalus Cleiothyridina	HF VHF MED LF	2	0.15				
20	Syringopora Crinoid	HF VHF	2	0.15				
19	Zaphrentis Syringopora Echinoid Orthotetes	IF HF VHF IF-VLF	2	0.14				
18	Zaphrentis Syringopora Crinoid Echinoid	IF HF VHF MED	2	0.10				
17	-	-	-					
16	Crinoid	VHF	1	0.07				
15	-	-	-	0.08				
14	-	-	-	0.05				
13	Crinoid	VHF	1	0.07				
12	Crinoid	VHF	1	0.05				
11	-	-	-	0.05				
10	Crinoid	VHF	1	0.03				
9	Crinoid Euomphalus	VHF MED	1	0.34				
8	Crinoid	VHF	1	0.11				
7	Zaphrentis Aulopora Crinoid Euomphalus Cleiothyridina Unispirifer	IF VHF MED VLF IF	2	0.37				
6	Zaphrentis Aulopora Crinoid Orthotetes	IF VHF IF-VLF	2	0.33				
5	Syringopora	HF	2	0.06				
4	Crinoid	VHF	1	0.03				
3	-	-	-	0.36				
2	Syringopora Crinoid Composita	HF VHF LF	2	0.11				
1	-	-	-	0.35				

1 For explanation see page

2 For explanation see page